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Zooplankton Ecology and Palaeoecology in Nutrient Enriched Shallow Lakes

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Abstract

This study sought to determine the potential of sedimentary cladoceran assemblages for inferring changes in shallow lake ecological structure and function.

The first stage of the study aimed to isolate and quantify the main structuring forces of the contemporary zooplankton community. Zooplankton populations were sampled from 39 mesotrophic to hyper-eutrophic shallow lakes (<3 m average depth) in the U.K. and Denmark. Additionally, a suite of environmental variables, including: fish, macrophytes, algal crop, nutrient concentrations and water transparency were analysed. A variety of numerical techniques including constrained ordination and logistic regression were employed to determine whole community and individual species response to the environmental variation within the data set.

The sedimentary remains of zooplankton were then enumerated from the surface sediments of the 39 'training set' lakes. These data were compared with the contemporary counts. Despite differential preservation of sedimentary remains, the main factors structuring the assemblages were the same in both data sets, zooplanktivorous fish density (ZF) and submerged macrophyte abundance (MA). Furthermore, these factors displayed a similar degree of influence on both assemblages.

A multivariate regression tree (MRT) was used to calibrate sedimentary cladoceran assemblage response to ZF and MA. The resultant model places a site in one of five groups based on cladoceran assemblage and corresponding to a range of values of ZF and MA. These groups represent distinct forms of ecosystem structure and function varying from sites with clear water, abundant macrophytes and low ZF to turbid, phytoplankton dominated systems with high ZF. Sedimentary cladoceran assemblages from dated cores for two sites, Felbrigg Lake (Norfolk, England) and Kenfig Pool (Glamorgan, Wales) were analysed. The cladoceran inferred ZF and MA indicated that both sites have undergone dramatic changes in ZF and MA. Comparison with plant macrofossil data and historical records at both sites indicated the veracity of the model.

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Glossary of Acronyms

SA	Surface area
EC	Electrical conductivity
SRP	Soluble reactive phosphorus
TP	Total phosphorus
Chla	Chlorophyll-*a*
NO3-N	Nitrate
SD	Secchi depth
PVI	Macrophyte percentage volume infestation
APVI	August macrophyte percentage volume infestation
MPVI	Mean macrophyte percentage volume infestation
DO	Dissolved oxygen
ZF	Zooplanktivorous fish
PF	Piscivorous fish
BF	Benthivorous fish
OW	Open water
L	Lake edge
WL	Whole lake
C	Contemporary samples
S	Surface sediment samples
DCA	Detrended correspondence analysis
CCA	Canonical correspondence analysis
RDA	Redundancy analysis
MRT	Multiple regression tree

1 Chapter 1 - Introduction

1.1 Background

The Earth's freshwater resources have long been exploited and modified by human activity. In the last two centuries aquatic systems have been subject to an increasing diversity of anthropogenic impacts. These include physical modification, increased nutrient (principally phosphorus and nitrogen) loading, deposition of acidifying substances, such as sulphate and nitrate and contamination by xenobiotic chemical compounds. The long range atmospheric transport of pollutants and the alteration of the Earth's atmosphere, related to increased levels of greenhouse gases, may mean that there are no aquatic systems, no matter how isolated, that remain unchanged by human activity (Smol et al. 2005). Arguably the most pervasive impact on aquatic systems results from increased plant nutrient loading, a phenomenon known as eutrophication. Over the past 100 years, in particular, eutrophication has induced profound changes to freshwater ecosystems (Mason & Bryant 1975, Moss 1977, Battarbee 1978, Sayer et al. 1999, Wetzel 2001). In general elevated nutrient concentration in lentic systems stimulates primary productivity, either through higher plant biomass or more commonly through an increased phytoplankton crop (Schindler 1974). In addition, there is a concomitant shift in algal community composition with blue-green algae increasingly likely to dominate (Watson et al. 1997).

1.2 Shallow lakes

Shallow lakes, defined as having an average depth of less than 3 m (Scheffer 1998), are especially susceptible to eutrophication. This vulnerability stems, in part, from their shallowness which results in relatively small volumes of water in these systems and thus a limited potential for dilution of pollutants. Shallow lakes, both artificial and natural in origin, are ubiquitous features of lowland Europe. In these landscapes that are often ecologically depauperate these lakes may provide relative 'hot spots' of biodiversity. They not only provide habitat for aquatic species, but also function as important foraging areas

for terrestrial animals and waterfowl (Jeppesen & Sammalkorpi 2001). Furthermore, shallow lakes and their associated wetlands may be of great socio-economic importance resulting from conservation value and tourism (Moss 2001).

Historically, limnological research has focused on large, deep lakes deemed important due to their size. However, whilst the total volume of lakes may be dominated by a few large deep sites, most are small and shallow (Wetzel 2001, Hughes et al. 2004). There are many differences in the physical and ecological functioning of deep and shallow lakes and in recent years the latter have increasingly become the subject of research (e.g. Scheffer 1998). A mean depth of less than 3 m results in the majority of the lake bed being available for colonisation by aquatic plants. In addition shallow lakes do not generally undergo thermal stratification. In deep lakes thermal stratification leads to the formation of the hypolimnion which isolates the pelagic photic zone from the, often nutrient rich, sediments. In shallow lakes the benthic and the pelagic zones are much more tightly linked (Jeppesen 1998). The photic zone often reaches the sediments, thus benthic forms of production may equal or exceed pelagic productivity (Liboriussen & Jeppesen 2003, Vadeboncoeur et al. 2003). Furthermore, the lack of separation between the surface waters and the sediment leads to increased potential for the recycling of nutrients and lack of exclusion of fish from the hypolimnion (Jeppesen et al. 1997b).

1.2.1 Definition of terms

As shallow lakes have a mean depth of less than 3m the entire lake could be classified as littoral. It is, therefore, necessary to set out clearly the definitions of the terms used in this thesis. Pelagic/planktonic and benthic/littoral are used to describe species' habitat preferences. Species defined as benthic or littoral are those associated with the sediment and/or plant surfaces. Those defined as pelagic/planktonic show a preference for the open water, free of physical structure. In terms of primary production, pelagic and planktonic refer to production by phytoplankton whereas benthic refers to non-planktonic productivity by attached forms of algae associated with the surface of the sediment or of macrophytes. In chapter 2 the zooplankton populations sampled from two areas of the study sites are compared. These different habitats sampled are termed the open water and lake edge. Open water describes the central area of the lake which may or may not contain a significant

number of plants. Lake edge is employed to define the 'littoral' area at the margins of the lake representing up to one or two metres away from the shore or emergent vegetation.

1.3 Shallow lake ecology and response to eutrophication

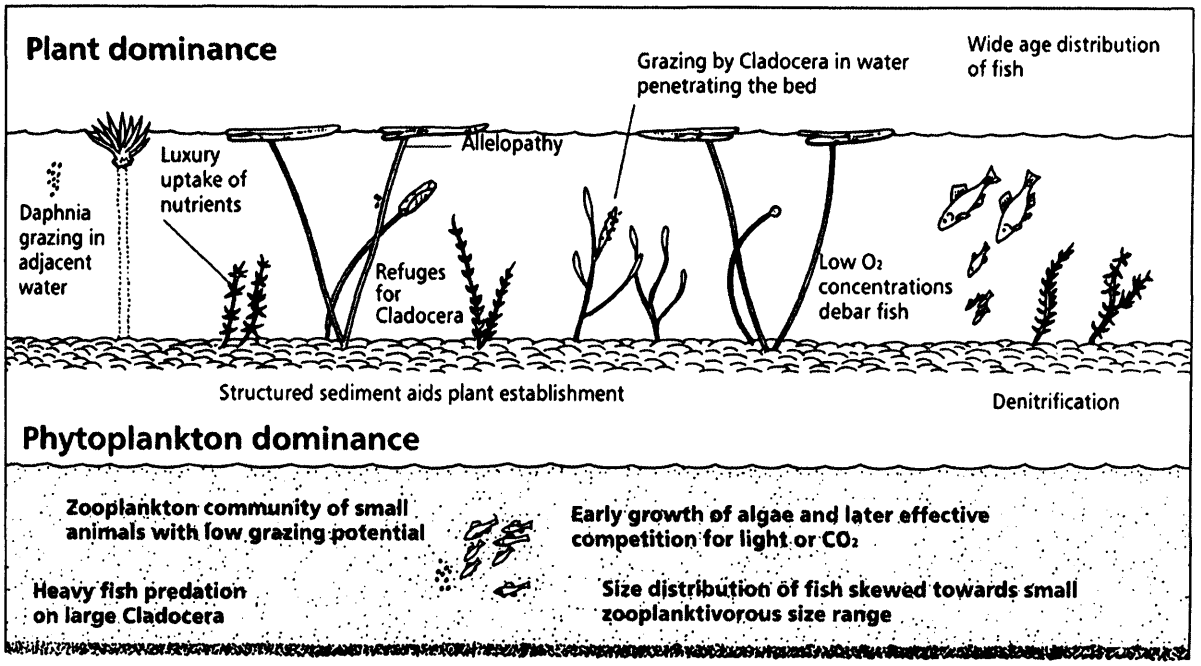
The close benthic-pelagic coupling in shallow lakes results in a complex response to eutrophication (Jeppesen 1998). Whilst elevated nutrient concentrations may increase primary productivity; food web interactions, the cascading effects of fish predation and herbivory can regulate ecosystem state and thus determine algal crop (Carpenter et al. 1985, Moss et al. 1994). In addition submerged plants, capable of colonising the majority of the lake bed, influence biological interactions at all trophic levels (Timms & Moss 1984, Carpenter & Lodge 1986, Diehl & Kornijów 1997, Søndegaard & Moss 1997). Research over recent decades has indicated that shallow lakes generally occupy one of two ecological states. The first is characterised by clear water and abundant submerged macrophytes; the second by turbid water, phytoplankton dominance and the absence of plants (Fig. 1-1) (Irvine et al. 1989, Moss 1989, Jeppesen et al. 1990). Scheffer et al. (1993) proposed that within an intermediate range of nutrient levels, these two states are alternatives. That is, there is a hysteresis in ecosystem response to any change in nutrient load with each state being 'buffered' against change by a number of biological feedback mechanisms (Fig. 1-1). Thus, whilst nutrients 'set the scene' and contribute to the likelihood of a shallow lake occupying one state or the other, it is the feedback mechanisms which actually maintain clear water or turbid conditions. Isolating the factors responsible for the breakdown of these buffering mechanisms, resulting in a switch to the alternative state, has proven difficult (e.g. Moss 1977, Phillips et al. 1978, Stansfield et al. 1989, Jones & Sayer 2002). It is clear, however, that submerged plants and fish community composition both directly and indirectly influence shallow lake ecological state (De Nie 1987, Norlin et al. 2005).

1.3.1 The role of fish

Fish are critical in determining the structure, function and stability of shallow lake ecosystems (Persson et al. 1988, Lammens 1999). They exert their influence through feeding strategies, in the pelagic and benthic food webs, by predation on herbivorous invertebrates which feed on epiphyton and phytoplankton. Zooplanktivorous fish

selectively feed on the larger zooplankton, both species and individuals, thus the dominance of such fish results in a population dominated by smaller taxa and individuals (Brooks & Dodson 1964). Field observations and experimental manipulations indicate that 'fish effects' cascade to the lower trophic levels, influencing zooplankton and invertebrate populations, phytoplankton biomass and even nutrient availability (Carpenter et al. 1985, Brönmark & Weisner 1992, Breukelaar et al. 1994, Jeppesen et al. 1998, Pace et al. 1999, Jones & Sayer 2002). Piscivorous fish can play an important role in controlling populations of zooplanktivorous fish. Thus, a reduction in piscivorous fish abundance and an increase in the proportion of zooplanktivorous and/or benthivorous fish is thought to exacerbate the effects of nutrient-enrichment and may be influential in inducing the 'switch' from a clear water, submerged vegetation-dominated state to a turbid, phytoplankton-dominated state (de Nie 1987, Brönmark & Weisner 1992, Jeppesen 1998).

Figure 1-1. The alternative states of plant and phytoplankton dominance and the biological feedback mechanisms buffer change from one state to the other (Figure from Moss et al. 1996a).



1.3.2 The role of submerged macrophytes

Submerged plant species play a key structuring role in shallow lakes influencing a variety of physical, chemical and biological processes connected to maintaining the clear water state (Carpenter & Lodge 1986). Their impacts are varied and include creating

heterogeneity in redox values in the sediment, promoting denitrification, and decreasing turbidity by increasing sediment settlement rates (Barko & James 1997). Some plant species, in particular charophytes, sequester phosphorus directly from the water column by binding it to precipitated carbonate (Blindow et al. 2002). In addition to direct effects aquatic plants also have indirect effects on ecosystem structure by the modification of the competitive advantage and predator prey relationships. For example, submerged and floating leaved species provide living substrata for plant-inhabiting invertebrates and refuge from predation for large bodied cladocerans (Lauridsen et al. 1996, Burks et al. 2002). This promotes clear water conditions by increasing grazing pressure on epiphytes and phytoplankton respectively (Timms & Moss 1984, Jeppesen et al. 1997a). Submerged and emergent aquatic plants provide essential hunting habitat for pike (*Esox lucius* L.) resulting in predation on zooplanktivorous fish (Søndergaard et al. 1997). In addition macrophytes provide a competitive advantage of young perch (*Perca fluviatilis* L.) over roach (*Rutilus rutilus* L.) and bream (*Abramis brama* L.) (Diehl 1988). Perch go through an ontogenetic niche shift and become piscivorous upon attaining a gape size sufficient to feed on smaller fish, at which point they prey effectively on small zooplanktivorous cyprinids, such as roach, rudd and bream (Persson & Crowder 1997). Thus, the structured habitat provided by submerged macrophytes promotes higher levels of piscivory which promotes clear water and in turn the dominance of plants. Conversely where plants are absent benthic and zooplanktivorous fish species have a competitive advantage over perch. Refuge from predation for large bodied cladocerans is absent and a turbid system where phytoplankton dominates becomes more likely.

1.3.3 Benthic to pelagic shifts in production

The primary productivity of shallow lakes in pristine, or minimally impacted condition is characterised by the dominance of benthic forms of production (Moss et al. 2003). As nutrient load increases there is an erosion of benthic pathways of production and the proportion of pelagic production rises (Vadeboncoeur et al. 2003). Elevated epilimnetic nutrient concentrations may result in a shift in the composition of the macrophyte community (Blindlow 1992, Moss 1999) and a reduction in its species richness (James et al. 2005). As the loading of phosphorus and nitrogen increase the maintenance of clear water conditions becomes dependent upon a number of biological feedback mechanisms (Moss 1989, Jeppesen 1998, Jeppesen et al. 2000). For example, a high proportion of

piscivorous fish suppresses zooplanktivorous fish density allowing the profusion of herbivorous cladocerans (Berg et al. 1997) which keeps grazing pressure on phytoplankton high (Timms & Moss 1984, Carpenter et al. 1985). With progressive eutrophication, therefore, the shallow lake ecological state may remain the same, the ecological function, however, progressively changes as the proportion of pelagic productivity increases (Vadeboncoeur et al. 2003). This alteration in function may be not be measurable in terms of a change in pelagic primary productivity as phytoplankton chlorophyll-*a* is reduced to low levels due to intense herbivory. The zooplankton community composition and abundance, however, has the potential to reflect these key eutrophication related shifts in shallow lake ecological function.

1.4 Zooplankton ecology in shallow lakes

Zooplankton is a key component of lentic ecosystems occupying a central position in the shallow lake food web and playing an important role in the determination of ecological state (Lynch & Shapiro 1981, Timms & Moss 1984, Moss et al. 1994). The term zooplankton refers to a number of different types of organism, *inter alia*: Cladocera (Branchiopoda), copepods (Copepoda) and rotifers (Rotifera). They are generally involved in secondary production, consuming algae or bacteria. In this thesis zooplankton refers to cladocerans and copepods; rotifers did not form part of this study as they leave few sedimentary remains.

Zooplankton, particularly cladocerans, can be divided into two groups: pelagic species, such as *Daphnia* spp., *Ceriodaphnia* spp. and *Bosmina* spp. and benthic species, typically chydorids, but including some larger bodied species, such as *Simocephalus* spp. The two groups tend to occupy different habitats within a shallow lake (Lauridsen et al. 1996). As their name suggests the pelagic species tend to live in open water occupying the same habitat as zooplanktivorous fish and are, thus, subject to more intense fish predation. In contrast, benthic species associated with plants or the sediment-water interface are reported to be less prone to predation by generally pelagic zooplanktivorous fish (Whiteside 1970).

Owing to their central position in the food-web the zooplankton community is influenced by multiple structuring forces. For example, food quantity (Vanni 1987), quality, (Gliwicz & Lampert 1990, Ghoudani et al. 2003) and the fish community influence the abundance and composition of zooplankton assemblages (Hrbácek et al. 1961). Brooks and Dodson (1965) investigated the effect of an introduced planktivore (the 'alewife', *Alosa psuedoharengus* Wilson.) on the body size and species composition of the planktonic cladoceran community. This work led to the development of the size-efficiency hypothesis, which states that fish feed selectively on the largest possible prey (Gardener 1981, Cryer et al. 1986). Aquatic macrophytes also structure the zooplankton community both through modification of the predator prey relationship (Timms & Moss 1984) and through provision of habitat and food for plant associated species (Lauridsen et al. 1996).

It is clear that there are a number of key elements determining the structure and functioning of shallow lakes. These same elements have significant direct and indirect effects on the cladocera community. There is potential, therefore, to use shifts in zooplankton community structure to model change in shallow lake ecosystems.

1.5 Zooplankton palaeoecology

Palaeolimnological techniques can provide insights into community and ecosystem dynamics over time scales unavailable to contemporary investigations (Anderson & Battarbee 1992). Such information may provide data on baseline conditions and natural variability allowing the isolation of anthropogenic influence (Smol 1992). Analysis of sub-fossil remains of cladocerans, such as carapaces, post-abdomens, claws, mandibles, sections of antennae and ephippia in both surface sediments and older core material is well established (Frey 1958, 1960a, Whiteside 1970, Kerfoot 1974, Hann 1989, Duigan & Birks 2000, Korhola & Rautio 2000, Jeppesen et al. 2001).

There are a number of taphonomic issues, however, which preclude the direct comparison of contemporary and sedimentary cladoceran assemblages. These include differential production of chitinous and ephippial remains and spatial heterogeneity of sedimentary

sub-fossils. Cladocerans shed their chitinous exo-skeleton as they grow and thus a single organism may produce many sub-fossil remains within its lifetime (Hann 1989). Research, on laminated sediments, has demonstrated chitinous remains accurately reflect the contemporary community that formed them (Hann et al. 1994, Leavitt et al. 1994). In contrast to chitinous remains, ephippia are the product of sexual reproduction, which typically occurs once or in some cases twice in a year (Korhola & Rautio 2000). Historically there has been a bias towards the use of chitinous remains in palaeoecological studies (e.g. Frey 1958) In spite of the fact that a number of keystone pelagic species, in particular the large bodied *Daphnia*, are poorly represented by chitinous remains (Korhola & Rautio 2000). More recently, however, studies analysing larger volumes of sediment have included the ephippial remains of these species (Jeppesen et al. 1996, 2001, Amsinck et al. 2005). Indeed it has been demonstrated that the relative abundance of *Daphnia* ephippia in surface sediments accords well with their contemporary relative abundance (Jeppesen et al. 2003a). Deep lakes display a degree of spatial heterogeneity of remains in surfaces sediments, with no single sample representing a complete integration of the pelagic and littoral fauna (Frey 1988). In contrast shallow lakes generally have relatively uniform basin morphology and less or no separation between pelagic and benthic species. Thus, a single sediment sample from the centre of a site may be sufficient to characterise the ecological variation within shallow lakes (Amoros & Jacquet 1987, Jeppesen et al. 2003a).

Sub-fossil cladoceran assemblages have been employed to track ecosystem change resulting from a multiplicity of factors. These have included changes in macrophyte coverage (Thoms et al. 1999), trophic state (Boucherle & Züllig 1983, Stansfield et al. 1989, Hofmann 1996), lake-level (Sarmaja-Korjonen & Alhonen 1999), saline transgressions (Sarmaja-Korjonen & Hyvärinen 2002) and an acidification event (Sarmaja-Korjonen & Hyvärinen 2002). Reflecting the direct relationship between the fish community and pelagic zooplankton, cladoceran sub-fossils have also been employed to infer temporal shifts in fish predation using relative abundance of cladoceran taxa (Leavitt et al. 1989, Leavitt et al. 1994, Miskimmen et al. 1995), length of body parts (Kitchell & Kitchell 1980, Kerfoot 1974, Kerfoot 1981, Hann et al. 1994) and numbers and size of ephippia (Verschuren & Marnell 1997, Jeppesen et al. 2002). More recent work combining contemporary ecology and palaeoecology in Denmark has used a surface sediment training

set of 30 lakes to develop a quantitative transfer functions for reconstructing zooplanktivorous fish predation pressure (Jeppesen et al. 1996) and macrophyte abundance (Jeppesen 1998).

Palaeolimnological inference models based on the transfer function approach have been employed to quantitatively reconstruct various aspects of past environments (Imbrie & Kipp 1971, Thompson 1981). These techniques have been applied to freshwater ecosystems, where the initial focus was on reconstructing past lake water pH from fossil diatom assemblages (Flower & Battarbee 1983, Jones et al. 1989, Battarbee 1990, Birks et al. 1990). The method involves the calibration of surface sediment biological assemblages, usually >30, against modern environmental data, typically collected over one year. Species optima and tolerance are determined for the chemical variable of interest, typically by regression (ter Braak & Prentice 1988, Birks et al. 1990). The transfer function then provides quantitative estimates of past values derived from the weighted averaging of the optima and tolerance of taxa in fossil assemblages. Thus, the fossil assemblage, via the transfer function, becomes a proxy for the past value of the modelled variable.

Since their inception numerous transfer functions have been developed and applied using various biological groups including diatoms (Birks et al. 1990, Fritz et al. 1991, Juggins 1992, Bennion et al. 1996), cladocerans (Jeppesen et al. 1996, Brodersen et al. 1998) and chironomids (Brodersen & Lindegaard 1999, Brooks & Birks 2000). The accuracy, and in some cases appropriateness, of these techniques has been increasingly questioned (Fritz et al. 1993, Bennion 2001, Jeppesen et al. 2001b, Sayer 2001, Brodersen et al. 2004, Velle et al. 2005, Battarbee et al. 2005a). For example, the zooplanktivorous fish transfer function developed by Jeppesen et al. (1996) was constructed using six pelagic taxa and apparently performed well. The predictive accuracy, however, declined in the presence of macrophytes (Jeppesen et al. 1996, Jeppesen et al. 2001b). There are a number of assumptions entailed in the transfer function approach (Birks & Gordon 1985, Birks et al. 1990, Juggins 1992), contravention of which may result in inaccuracies in inferred values. One of the key assumptions of the transfer function approach is that environmental variables, other than the one of interest (such as, zooplanktivorous fish density), have negligible influence or their joint distribution in the fossil set is the same as in the training set. Given the central position of zooplankton in lentic food-webs and the close benthic-pelagic coupling of

shallow lakes a transfer function based solely on pelagic or benthic species is extremely unlikely to meet this assumption. Fish and macrophytes affect shallow lake ecosystem function and zooplankton community composition and both are influenced by eutrophication (Blindlow 1992, Moss 1999, James et al. 2005, Mehner et al. 2005). Consequently, it is unlikely that either parameter will change in isolation. There is, therefore, a clear need to asses the potential of other modelling techniques which might allow the simultaneous reconstruction of more than one variable.

1.6 Overall aim and specific research questions

The ultimate aim of this thesis is to explore the potential of sub-fossil cladoceran to model the ecological structure and function of shallow lakes. To this end, a number of specific research questions were addressed, as follows:

- What structures the contemporary zooplankton population in 39 shallow lowland lakes?
- Are these structuring forces the same for surface sediment assemblages, despite differential preservation of various taxa?
- Can cladocera communities be used to model and therefore infer changes in these structuring elements?
- How does the ecological structure and function, reflected by changes in macrophyte abundance and zooplanktivorous fish density, change in two shallow lakes in response to eutrophication?

1.7 Study sites

Thirty nine sites were selected for study with 29 lakes in Norfolk U.K. (Fig. 1-2) and 10 in Denmark, (6 in Jutland, 3 in Southern Zealand and 1 on Falster) (Fig. 1-3). The 29 U.K. sites were selected from a larger dataset, based on preliminary studies of nutrient chemistry, macrophyte community and, where available, fish community data. The sites were selected to represent long and evenly spaced gradients of the most ecologically significant variables

with particular emphasis on nutrient concentration, submerged macrophyte abundance and fish community composition and abundance (Fig. 1-4). A further ten sites from Denmark were included with the aim of providing more sites at the low end of the nutrient gradient. The ranges and means (for April to September) show that there was a good variation in the key environmental variables between sites (Table 1-1). Whilst the Danish sites, in general, had lower nutrient concentrations principal components analysis (PCA) of the main chemical and biological variables did not reveal any inherent geographic bias (Fig. 1-5). The integrity of the surface sediments of each site was of vital importance, therefore sites with undisturbed sediments were chosen. There were, however, three sites, two within the Norfolk Broads, Cockshoot and Strumpshaw Broads, and one estate lake, Bayfield Hall Lake, which had been dredged as part of management strategies (Moss et al. 1996a, 1996b, Moss 2001). At Cockshoot Broad the surface sediments were extracted from an un-dredged area. At Bayfield Hall Lake and Strumpshaw Broad, where dredging occurred more than 20 years ago, sufficient time was considered to have passed since sediment removal for the surface sediments to represent the accumulation of recent remains only.

The training set sites are all artificial in origin, with the exception of Saham Toney Mere, which is a kettle-hole lake. A number of sites are part of the Norfolk Broads system formed as a result of the flooding of medieval peat diggings in the 12^{th} to 14^{th} centuries (Moss 2001). A small number of the Danish sites are more recent peat diggings, between 70-100 years old. Other origins include medieval 'stew' ponds (used for rearing fish) of which Felbrigg Lake (FELB) is one, ornamental country 'estate' lakes, such as Wolterton Hall Lake (WOLT) constructed in the late eighteenth to mid-nineteenth century, mill ponds and duck decoy ponds.

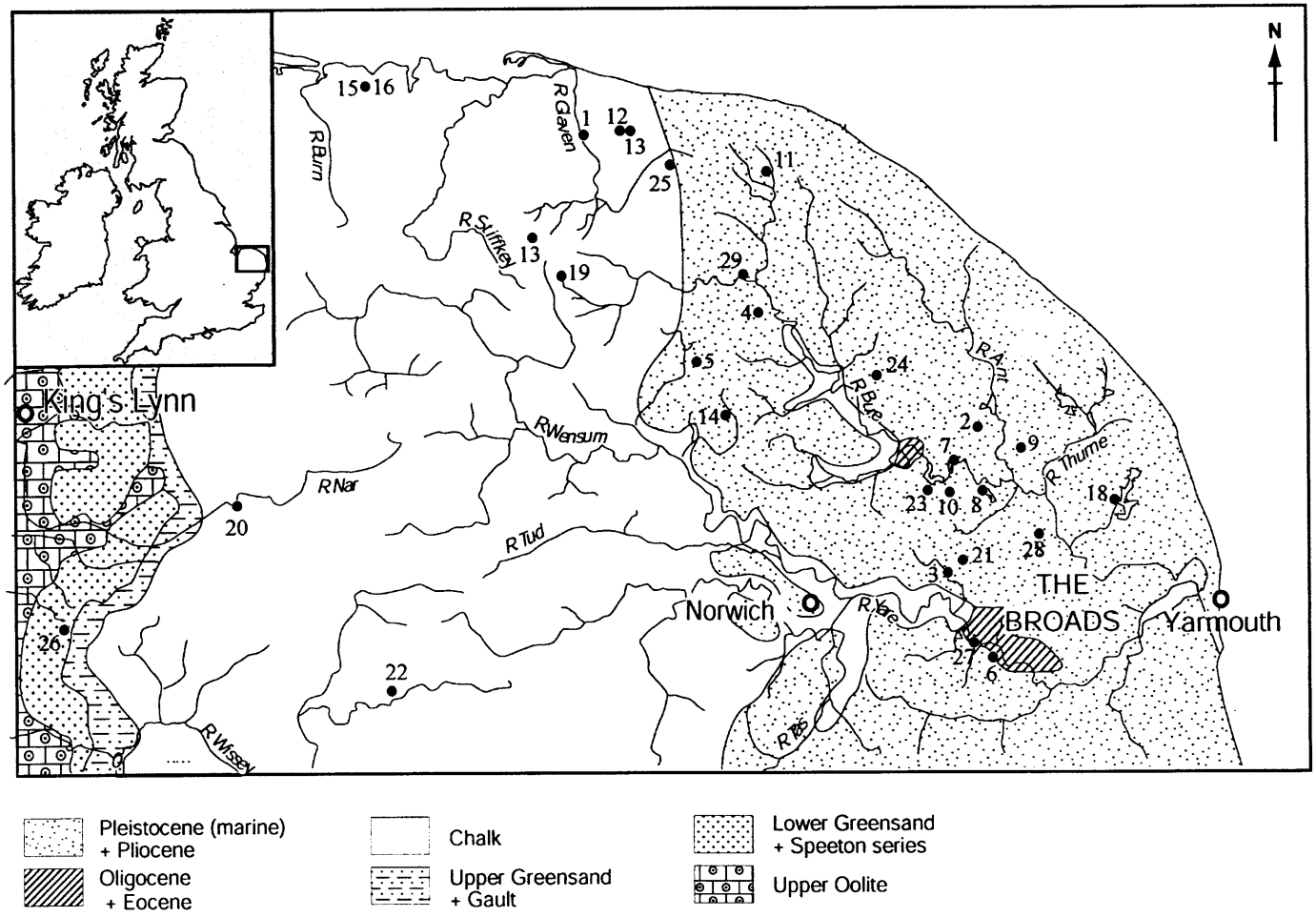
Geologically the two regions sampled were similar. Norfolk has two main geological regions with Cretaceous chalk deposits to the west and Pleistocene and Pliocene sands and clays to the east. In Denmark the sites in the undulating landscape of east Jutland were formed by the moraines and outwash left by the retreating glaciers at the beginning of the current interglacial period. The resulting geology is one of loams and clays. In southern Zealand, and on the island of Falster, the geology is dominated by Cretaceous chalk and limestone. The analogous geology of the two areas results in sites with similar background chemistry, characterised by high alkalinity and generally high conductivity (Table 1-1).

Fossil cladoceran assemblages were analysed from sediment cores from two sites. The first, Felbrigg lake (TG 191 388) is a shallow (max. depth=150 cm), small (2.7 ha), lowland 'estate' lake, in the grounds of Felbrigg Hall, North Norfolk. It formed part of the 'training set' of 39 sites in this study. Its origins were as a number of small 'stew ponds' stocked with carp (*Cyprinus carpio* L.) and tench (*Tinca tinca* L.) in the 17th century. The other is Kenfig Pool (SS 790 820) a shallow (max. depth=2.6) moderately large (24 ha) lake situated within the extensive sand dune system of the Kenfig National Nature Reserve. The geology is base rich consisting of limestone and marine derived sands.

1.8 Supporting data sets

The detailed characterisation of the physical, chemical and in particular the biological attributes of a relatively large number of shallow lakes was a vital part of this study. It was only possible to generate such a large data set via links with a number of research projects. These include a Natural Environment Research Council (NERC) Fellowship project (Sayer), a NERC small grant (Sayer) and from collaboration with Professor Eric Jeppesen at the Natural Environment Research Institute (NERI) in Silkeborg, Denmark. Zooplankton and sub-fossil cladoceran analysis and all numerical analysis were conducted by the author. In the U.K. the NERC fellowship provided the chemistry data (Jones & Sayer 2002, Sayer & Hughes unpublished data) and macrophyte data (Sayer & Davidson unpublished data). The fish data were generated as part of a NERC small grant (Perrow & Sayer unpublished data, Zambrano et al. submitted). In Denmark all survey work was carried out by the author and chemistry data were kindly provided by NERI (Jeppesen et al, unpublished data). The Ph.D. was stimulated by and owes a great deal to previous work on zooplankton and their sedimentary remains in shallow lakes, principally carried out in Denmark (e.g. Jeppesen et al. 1996, 1997a, 1999, 2001) and on a wealth of work on shallow lake ecology conducted over the past 20 to 30 years (e.g. Irvine et al. 1989, Scheffer et al. 1993, Moss 1999).

Figure 1-2. Location of 29 U.K. sites in Norfolk, England.



Pleistocene (marine) + Pliocene

Oligocene + Eocene

Chalk

Upper Greensand + Gault

Lower Greensand + Speeton series

Upper Oolite

1-Bayfield Hall Lake
2-Beeston Hall Lake
3- Big Wood Lake
4-Blickling Hall Lake
5-Bluestone Lake
6-Buckenham Broad
7-Burntfen Broad
8-Cockshoot Broad
9-Cromes Broad
10-Decoy Broad
11-Felbrigg Lake
12-Green Plantation Pond
13-Gunthorpe Hall Lake
14-Haveringland Lake
15-Holkham Hall Lake, isolated section
16-Holkham Hall Lake, main section
17-Lowes Pond
18-Lily Broad
19-Melton Constable Lake
20-Narford Hall Lake
21-Pedham Lake
22-Saham Toney Mere
23-Salhouse Little Broad
24-Scottow Pond
25-Selbrigg Pond
26-Stradsett Hall Lake
27-Strumpshaw Broad
28-Upton Broad
29-Wolterton Hall Lake

Figure 1-3. Location of the 10 Danish sites: 6 on Jutland, 3 on Zealand and 1 on Falster.

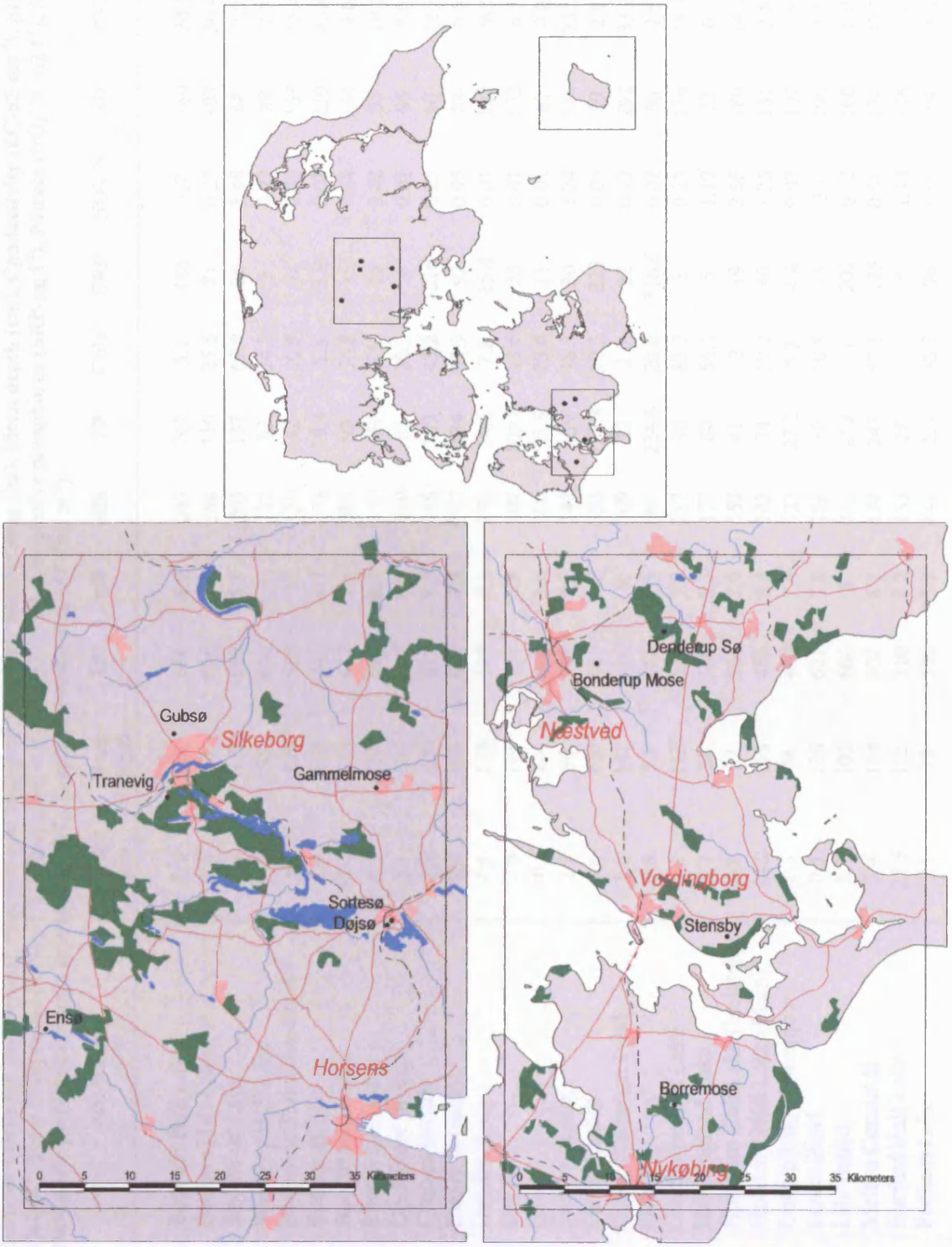


Table 1-1. Summer means for key physical, chemical and biological variables: Surface area (ha), Mean depth (cm), Conductivity (EC-μS cm^{-3}), pH, Alkalinity (Alk-mg l^{-1}CaCO$_3$), Total Phosphorus (TP-μg l^{-1}), Chlorophyll-*a* (Chla-μg l^{-1}), Soluble reactive phosphorus (SRP-μg l^{-1}), Nitrate (NO_3^--N-mg l^{-1}), Secchi depth (SD-cm), Macrophyte percentage volume infestation (PVI), Zooplanktivorous fish (ZF-fish m^{-2}).

Site code	Site Name	Surface area	Mean depth	EC	pH	Alk	TP	Chla	SRP	NO_3^--N	SD	PVI	ZF
BAYF	Bayfield Hall Lake	2.7	92	666	8.3	265	262	5.1	186	1.7	180	20.1	0.01
BEES	Beeston Hall Lake	2.6	61	616	7.7	162	110	25.5	21	0.23	107	36.4	0.54
BIGW	Big Wood Lake	4.3	67	692	8.1	203	137	69.9	20	1.48	68	7.9	0.84
BLIC	Blickling Hall Lake	10.1	95	480	9	112	83	34.2	3	0.22	89	7.3	0.26
BLUE	Bluestone Plantation Pond	3.6	120	516	8	150	42	10.9	6	0.09	163	18.4	2.24
BOND	Bonderup	1.9	213	443	8.3	173	19.4	8.3	3.8	0.01	230	45.4	2.56
BUCK	Buckenham Broad	0.4	123	632	8.1	216	92	56.8	15	0.64	144	9.0	1.53
BURF	Burntfen Broad	4.7	118	664	8.1	157	157	85	15	0.42	55	10.2	1.48
COSH	Cockshoot Broad	5.1	100	696	8.2	289	85	20.5	9	0.01	95	8.0	0.97
CROM	Cromes Broad	2.3	58	615	8.3	166	389	43.2	216	0.23	67	18.3	0.42
DECO	Decoy Broad	9.4	140	610	8.3	187	184	52.9	92	0.95	83	0.0	0.81
DEND	Denderup	4.5	139	395	8.1	171	54.6	7.2	15.4	0.01	182	26.9	0.00
DOJ	Døj Sø	2.0	108	384	8.3	107	109.8	18.6	33	0.01	152	6.4	0.05
ENSO	Ensø	10.6	204	346	8.6	106	75.8	29.6	11	0.01	81	0.0	0.37
FELB	Felbrigg Lake	2.7	90	508	8.7	142	139	18.3	30	1.24	119	23.9	2.44
GAMM	Gammlemose	1.6	110	447	8.7	153	157.4	78.5	223	0.03	89	2.0	0.18
GREP	Green Plantation Pond	1.6	147	516	8	109	22	2.3	22	0.79	292	33.2	0.00
GUB	Gub Sø	0.6	55	266	7.9	98	224.6	20.6	116.6	0.02	86	2.5	0.05
GUNT	Gunthorpe Hall Lake	1.7	113	522	7.7	212	98	83.7	3	0.28	136	18.4	1.58
HAVE	Haveringland Lake	4.7	58	566	8.3	177	80	56.6	5	1.19	72	0.0	3.26
HOKI	Holkham Hall Lake (Isolated)	0.8	82	564	7.9	159	41	2	19	2.66	180	14.7	0.00
HOKM	Holkham Hall Lake (Main)	14.2	146	456	8.4	143	74	19.2	40	1.25	131	3.5	0.00
LIST	Listrup lyng (Børremose)	1.5	78	480	7.8	137	27.2	5.2	4.4	0.02	107	5.8	0.45
LOPO	Lowes Pond	0.5	136	621	7.8	186	30	10.8	15	2.1	196	2.1	0.80
LYLI	Lily Broad	8.1	105	666	8	230	259	5.1	202	0.12	160	0.0	0.12
MELT	Melton Constable	7.4	124	308	8.7	128	243	57.1	125	0.01	138	13.7	0.01
NARF	Narford Hall Lake	22.5	105	310	8.2	135	28	4.5	4	1.43	196	9.6	0.04
PEDH	Pedham Lake	3.1	78	536	7.7	141	224	60.7	96	1.65	59	3.8	0.68

Site code	Site Name	Surface area	Mean depth	EC	pH	Alk	TP	Chla	SRP	NO_3^--N	SD	Mac	ZF
SAHA	Saham Toney Mere	5.3	156	524	8.5	175	560	29.3	243	0.01	97	0.0	0.02
SALH	Salhouse Little Broad	1.2	74	652	7.8	216	84	21	112	1.12	128	31.9	0.65
SCOT	Scottow Pond	2.0	85	654	7.5	179	51	5.5	7	0.2	160	45.7	0.01
SELB	Selbrigg Pond	3.1	83	590	7.6	202	34	5.3	7	0.01	145	30.5	2.09
SORT	Sorte Sø	4.6	65	1022	7.9	310	4056	44.6	3065	0.1	48	0.0	0.00
STEN	Stensby	1.0	54	533	7.8	227	37.6	2.8	3.6	0.01	184	17.2	0.49
STRA	Stradsett Hall Lake	8.3	109	438	8.7	101	283	17	157	0.12	141	34.6	1.74
STRU	Strumpshaw Broad	2.8	84	1378	8.5	177	151	7.6	73	0	126	34.1	0.47
TRAN	Tranevig	3.0	67	305	7.7	71	88.8	37.6	18.4	0.02	75	44.3	0.77
UPTO	Upton Broad	6.9	90	434	8.7	128	33	9.7	8	0	92	29.7	0.11
WOLT	Wolterton Hall Lake	4.1	84	494	8.3	124	63	13.1	28	0.01	226	19.7	0.00
	Mean	**22.5**	**103.0**	**552.4**	**8.2**	**167.3**	**227.9**	**27.8**	**135.2**	**0.5**	**130**	**16.3**	**0.71**
	Minimum	**0.4**	**54.3**	**266.3**	**7.5**	**71**	**19.4**	**2**	**3**	**0**	**48**	**0.0**	**0.0**
	Maximum	**4.6**	**212.6**	**1378**	**9**	**310**	**4056**	**85**	**3065**	**2.66**	**292**	**45.7**	**3.26**

Figure 1-4. Ranges of key chemical and biological variables of the 39 shallow lakes: A) TP ($\mu g\ l^{-1}$) Sørte Sø excluded, B) NO_3^--N ($mg\ l^{-1}$), C) Chlorophyll-*a* ($\mu g\ l^{-1}$), D) Secchi depth (cm), E) Macrophyte PVI (PVI), F) Zooplanktivorous fish density (no. m^{-2}).

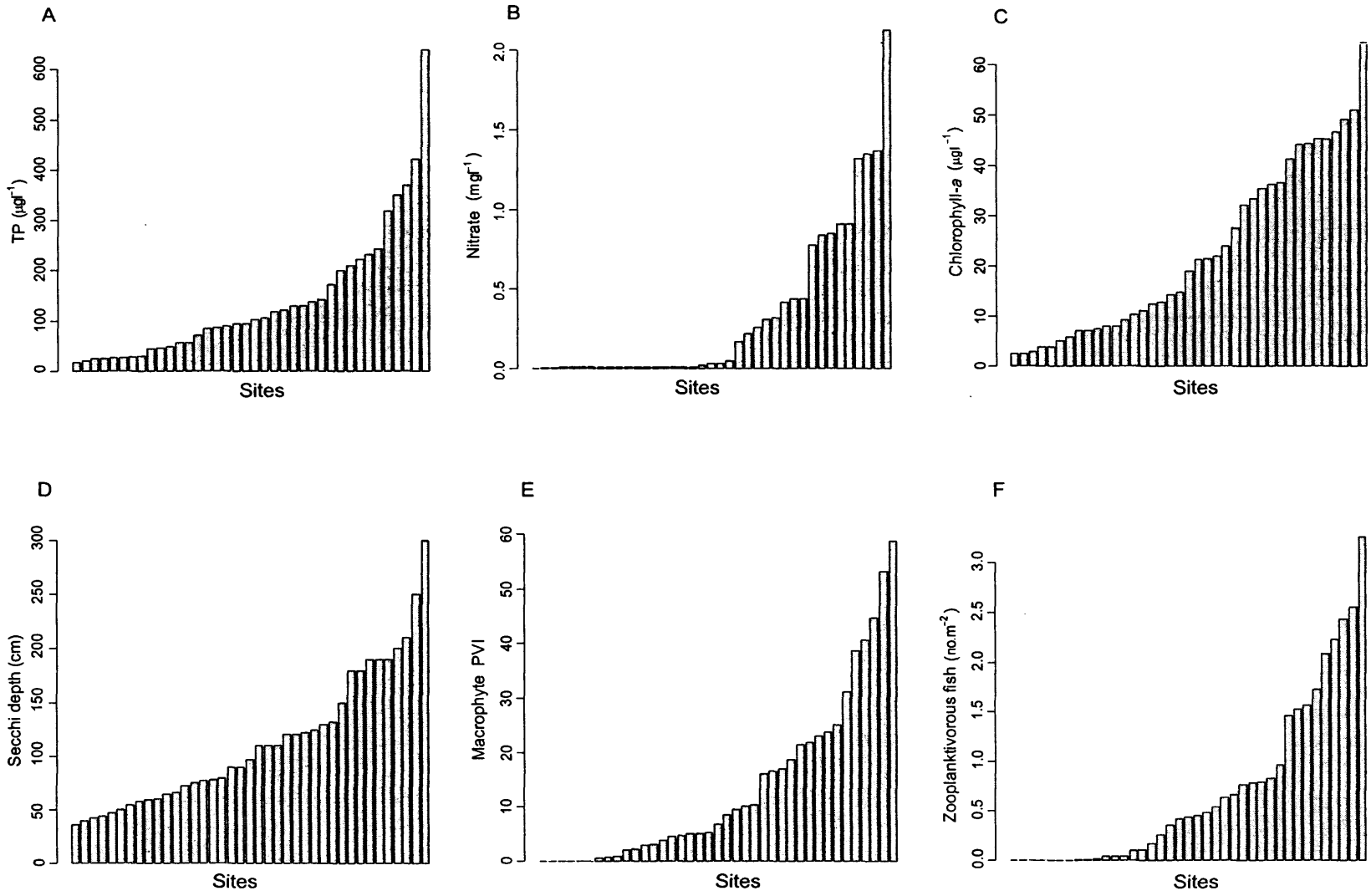
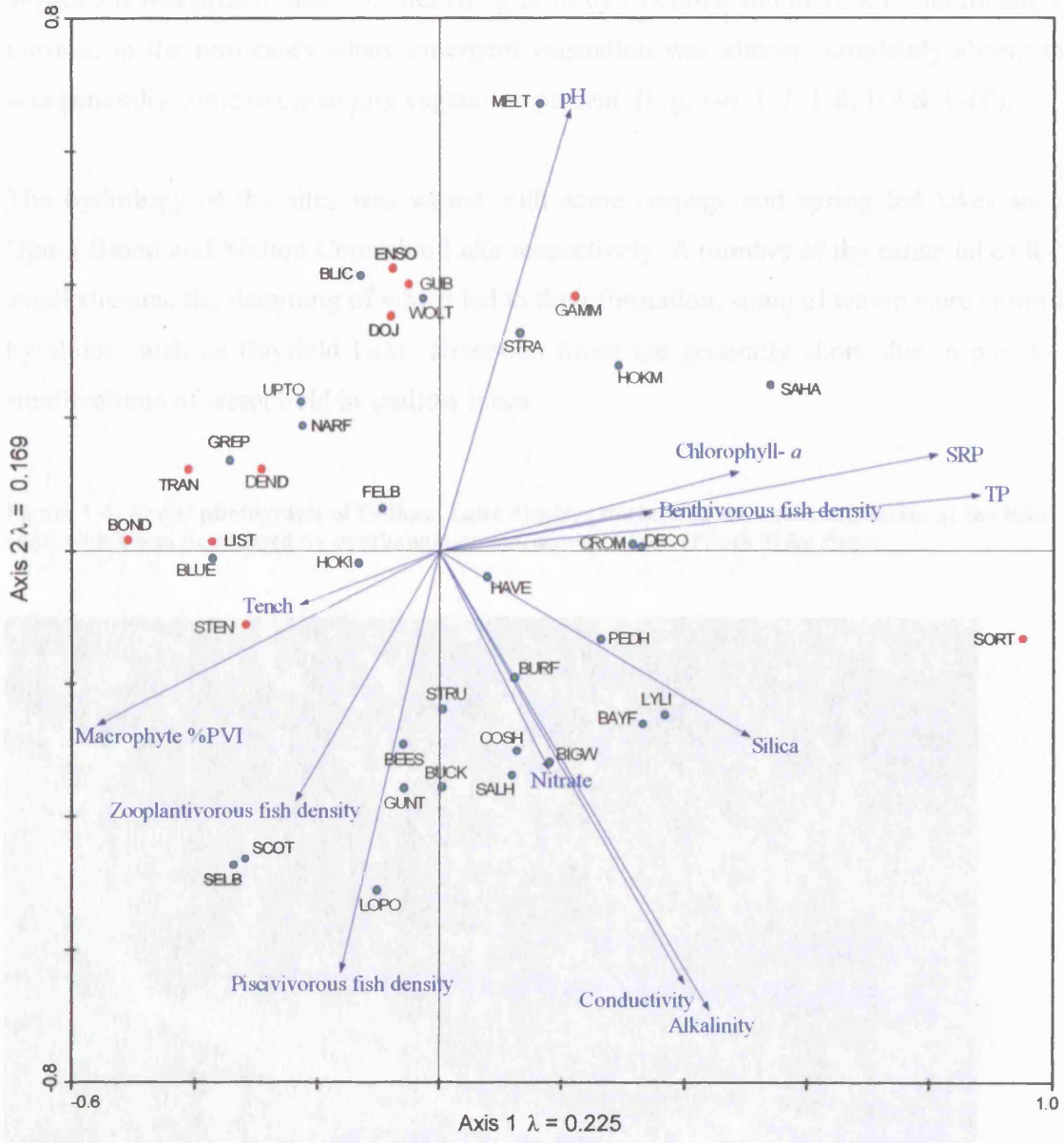


Figure 1-5. PCA of summer means of selected chemical and biological variables of the 39 sites: Conductivity (µS cm^{-3}), pH, Alkalinity (mg l^{-1} $CaCO_3$), Total Phosphorus (TP-µg l^{-1}), Chlorophyll-*a* (µg l^{-1}), Soluble reactive phosphorus (SRP-µg l^{-1}), Nitrate (mg l^{-1}), Silica (mg l^{-1}), Macrophyte PVI, Zooplanktivorous fish (no. m^{-2}), Benthivorous fish (no. m^{-2}), Piscivorous fish (no. m^{-2}), Tench (no. m^{-2}). Danish sites (●) and UK sites (●)



The sites are all relatively small (0.5-22 ha) and shallow with a mean depth of less than 3 m (Table 1-1). All lakes had a relatively uniform morphology. There were inter-site differences, however, in the nature of the lake edge. At some sites there are gentle slopes from the edge and at others, in particular the Broad sites, there is a sharp drop off to depths greater than 0.5 m. The physical nature of the lake margins varied considerably between sites. At some sites there were extensive stands of marginal vegetation such as *Phragmites*

australis Trin. ex. Steudel, *Typha latifolia* L., *Typha angustifolia* L., *Cladium mariscus* L., *Scheonoplectus lacustris* L. and *Carex* spp. In other cases, in particular the estate lakes, there was less physical structure in the lake margins. In some cases what emergent vegetation was present had been heavily grazed by livestock and there was significant bank erosion. In the rare cases where emergent vegetation was almost completely absent there was generally some overhanging vegetation present. (Fig. 1-6, 1-7, 1-8, 1-9 & 1-10).

The hydrology of the sites was varied with some seepage and spring fed lakes such as Upton Broad and Melton Constable Lake respectively. A number of the estate lakes fed by small streams, the damming of which led to their formation, some of which were controlled by sluice, such as Bayfield Lake. Retention times are generally short, due in part to the small volume of water held in shallow lakes.

Figure 1-6. Aerial photograph of Pedham Lake displays the lack of emergent vegetation at the lake edge, which was dominated by overhanging trees, mostly Alder. (Photo Mike Page).

Figure 1-7. Boat house and lake edge of a typical 'estate lake'. The emergent vegetation consists of a small patch of *Carex* spp. but is dominated by overhanging trees.

Figure 1-8. Estate lake showing ornamental *Nymphaea* species and lack of emergent vegetation.

Figure 1-9. Cromes Broad illustrating the extensive *Phragmites australis* dominated lake edge.

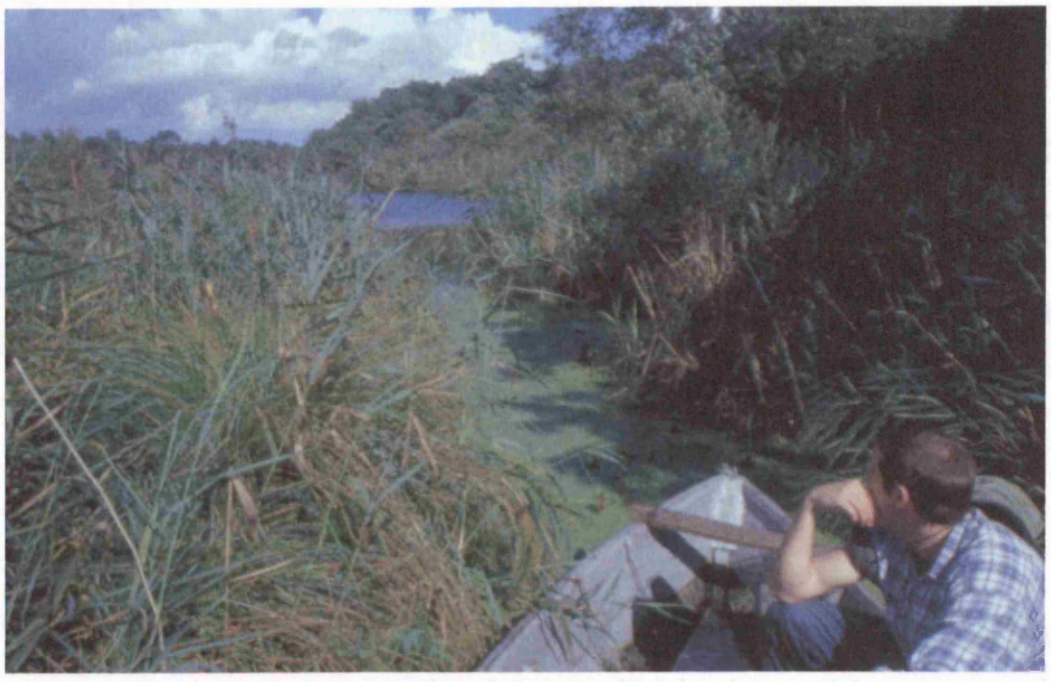


Figure 1-10 Felbrigg lake margin showing both a *Phragmites australis* reed bed and the near bank eroded by grazing livestock

1.9 Structure and outline of thesis

The four sections of this study (Fig. 1-11) represent a logical progression from the investigation of modern to fossil zooplankton assemblages. The findings of each stage inform the next phase, facilitating the interpretation of the observed patterns and validating the use of the techniques. The thesis is presented in a 'research paper' format, with each section of the study written in the form of a journal article, preceded by a general introduction and finishing with a concluding chapter, which summarise the findings and discusses possibilities for future work. Each section contains an introduction and a description and assessment of the methods employed therein.

This thesis is divided into four linked sections as follows.

Section 1 The factors determining the lake centre and lake edge zooplankton communities in August are analysed for the 39 lake data set. August was selected as it represents a peak period of production when macrophyte growth and fish predation are often at their peak in temperate shallow lakes (Jeppesen et al. 2003b). Multivariate and univariate statistical techniques are employed to analyse the patterns within the zooplankton data with the aim of isolating and where possible quantifying the factors determining the presence, absence and abundance of species.

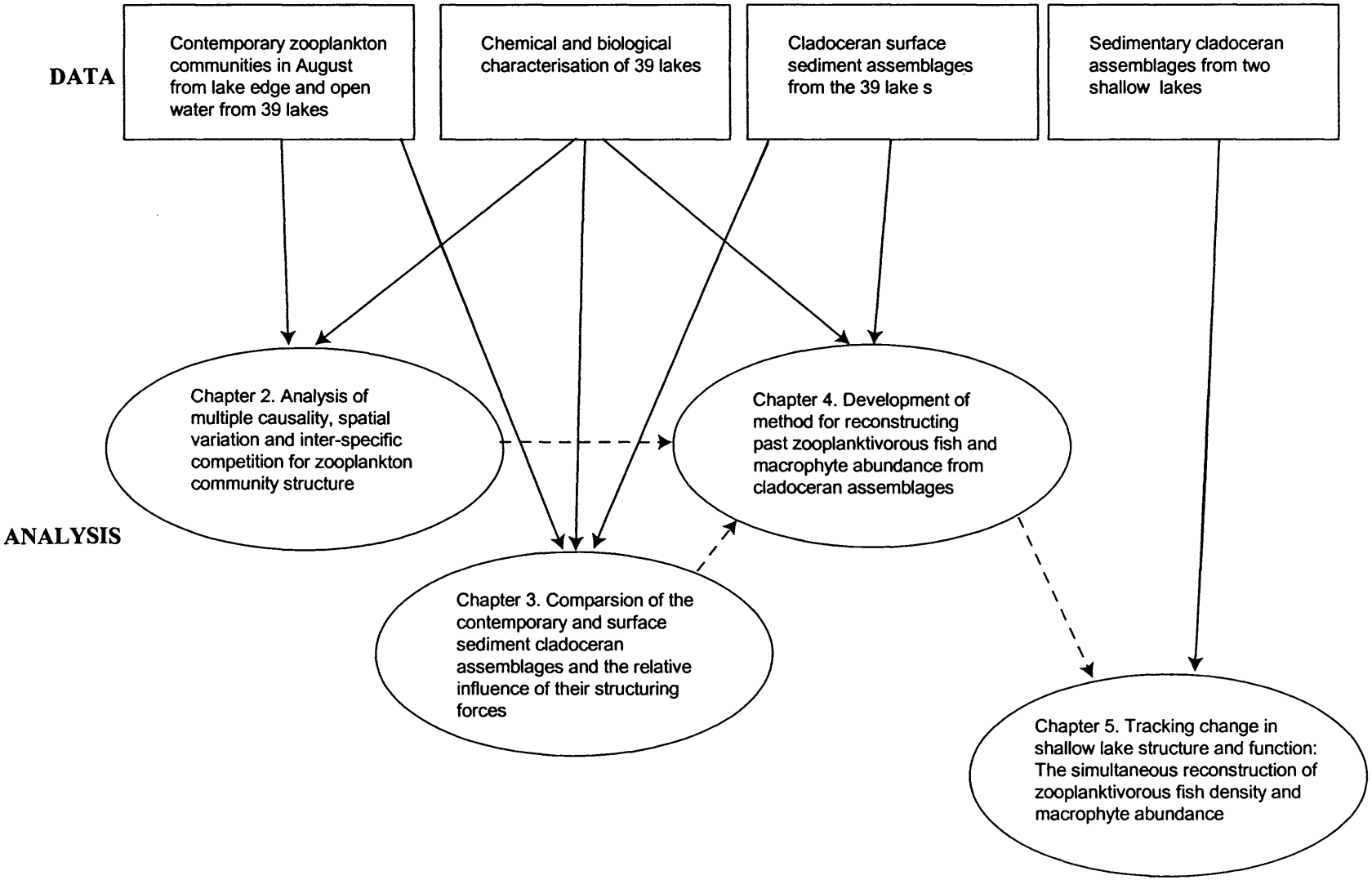
Section 2 Given the desirability of using principles and relationships established in the contemporary environment to interpret patterns in sedimentary data it is vital that the relationship between the two data sets is established. Thus, section 2 of the thesis compares contemporary zooplankton communities from August with the surficial sediment cladoceran assemblages from the 39 lakes.

Section 3 The first two sections of the thesis establish that a number of factors combine to determine whole community composition and the likelihood of occurrence of individual species. This precludes the use of the transfer function approach to palaeoecological inference modelling as it contravenes one of the key assumptions. In

section 3 a multivariate regression tree (MRT) is employed with the aim of developing a model capable of reconstructing two variables simultaneously.

Section 4 The model developed in section 3 is applied to the sedimentary cladoceran assemblages from two shallow lakes: Felbrigg Lake, Norfolk, one of the 39 study sites, and Kenfig Pool, south Wales which was not part of the data set used for model development. Documentary and macrofossil records are available for both sites providing information on past fish and macrophyte communities. These data are compared with the findings of the MRT inference model.

Figure 1-11. Conceptual diagram of the thesis structure. The rectangular boxes represent the sources of data. The ellipses represent the different sections/chapters of the thesis and the arrows signify the source of the data for each chapter and the flow of information from one section to another.



2 Chapter 2 - Zooplankton community structure in shallow lakes: multiple causality, spatial variation and inter-specific competition

2.1 Introduction

Zooplankton populations are a key component of aquatic ecosystems occupying a central role in the lacustrine food-web. Experimental and field-based work has demonstrated that various forces structure community composition and abundance (e.g. Brooks & Dodson 1965, Lynch 1978, Timms & Moss 1984, Vanni 1987, Lueke et al. 1990). The relative influence of 'bottom-up' and 'top-down' forces on aquatic systems as a whole has sparked much debate (Carpenter et al. 1987, McQueen et al. 1986). Bottom-up control refers to the limitation of primary production and shaping of ecosystem functioning by nutrient concentrations. In contrast, top-down control refers to a system where predation (vertebrate or invertebrate) and grazing determine ecosystem function and phytoplankton abundance is limited by herbivorous zooplankton (Carpenter et al. 1985, Moss et al. 1994). This polemic led to much early research into the forces structuring zooplankton communities, particularly pelagic species, with a focus on the relative importance of food limitation and predation pressure (e.g. Kerfoot 1977, Lynch 1979).

Feeding efficiency and tolerance of low food levels generally increase with cladoceran body size (Gliwicz 1990). Thus, competition for resources can result in large-bodied species dominating planktonic communities (Vanni 1986). Larger species are, however, more vulnerable to size-selective predation by zooplanktivorous fish (Brooks & Dodson 1965, Persson et al. 1988). Predation pressure can, therefore, exclude larger species and bigger individuals within a species, leading to a community dominated by small species, such as *Bosmina longirostris* Müller. The pelagic zooplankton community of a lake is, therefore, a reflection of the balance between these bottom-up (food source) and top-down

(predation pressure) forces (Vanni 1987, Leavitt et al. 1989, Carpenter et al. 1987, Gliwicz 2002).

In contrast to deeper lakes which may undergo thermal stratification, shallow lakes have a less distinct separation between benthic and pelagic zones. The effects of fish and macrophytes may be of particular importance in determining the zooplankton community (Jeppesen et al. 1997a). Submerged, floating-leaved and even emergent species of plants provide refuge from fish predation for larger pelagic cladocera (Timms & Moss 1984, Lauridsen et al. 1996). The larger free-swimming species, such as *Daphnia* spp. may use plants during the day and move into areas of open water at night when visual predation by fish is less effective, a phenomenon termed diel horizontal migration (Timms & Moss 1984, Burks et al. 2002). Macrophytes also provide habitat for a variety of poor swimming species (Quade 1969, Fairchild 1981, Lauridsen et al. 1996), which may exert a considerable influence on phytoplankton abundance (Stansfield et al. 1997, Bayala & Moss 2004). Several species display some plasticity in feeding behaviour and habitat preference. Experimental studies with the large *Daphnia magna* Straus indicate the species' disinclination to occupy plant beds in the absence of fish. The addition of fish cues, however, resulted in the species utilising the refuge from predation afforded by macrophytes (Lauridsen & Lodge 1996). Furthermore, food-web investigations employing stable isotopes, in particular carbon, indicated that the *Daphnia* guild may also feed extensively on periphyton as well as phytoplankton (Jones & Waldron 2003).

Food quality as well as quantity may affect community structure. The factors determining the phytoplankton community are complex. For example, intense grazing pressure by *Daphnia*, (Lampert et al. 1986) and/or an N:P ratio (Shapiro 1973, Ferber et al. 2004) may result in high proportions of cyanobacteria. The large filaments of blue-green algae can mechanically impede efficient feeding by larger zooplankton, in particular cladocerans (Gliwicz & Lampert 1990). There may, in addition, be a toxic effect (Lampert 1982). Thus, dominance of the phytoplankton by cyanobacteria may exclude larger species resulting in the population being dominated by smaller zooplankton, such as *Bosmina* spp. or *Chydorus sphaericus* Müller (Ghoudani et al. 2003).

It is clear that zooplankton community composition and abundance are not simply determined by one factor but by the interaction of a raft of variables exerting differing influence dependent upon lake type and trophic state (Pinel-Alloul et al. 1995, Jeppesen et al. 2003b, Vadeboncoeur et al. 2003). For example, Jeppesen et al. (2003b) assert that the presence of fish has a higher impact on the contribution of *Daphnia* spp. to the overall zooplankton biomass at low and high total phosphorus (TP) concentrations, whereas the fish effect is limited at intermediate TP levels. It is a simplification but also a truism that nutrient availability has an impact on aquatic system structure and function (Jeppesen et al. 2000). Shallow lakes display a non-linearity, or hysteresis, in response to nutrient enrichment (Scheffer et al. 1993). When change occurs, however, the ecological components (phytoplankton, zooplankton, fish, and aquatic plants) generally change in concert (Jeppesen et al. 2000, Brodersen et al. 2001). This synchronicity of change in the biological community composition and ecological function of shallow lakes makes the determination of the causal mechanism(s) responsible for change difficult to disentangle from those merely associated with it. Whittaker et al. (1973) termed the phenomenon of multiple correlated factors varying together as the 'complex gradient', applying it to the manifold changes associated with increasing altitude. In terms of shallow lake ecosystems TP or secchi depth may be analogous to altitude, summarising much change and being relatively easy to measure, whilst directly causing a very small proportion of change.

Studies which have set out to assess the relative importance of the different structuring forces on the zooplankton community have often been based on biomanipulation of one (McQueen et al. 1989) or a small number of lakes (Pace et al. 1998, Gliwicz 2002). Enclosure experiments simplify the system in order to isolate the influence of resource control (competition) and/or predation. The differing conclusions about the relative influence of bottom-up and top-down forces are due, at least in part, to the wide range of scale (temporal, spatial, lake depth and trophic level) over which studies have been carried out. With some notable exceptions (Pinel-Alloul et al. 1995, Jeppesen et al. 2003b) few studies have used an extensive set of field observations to assess the influence of chemical and biological gradients on zooplankton community structure. Furthermore, most studies, due to the historical predilection to study larger, deeper lakes, have tended to be biased towards pelagic communities or species. This study sought to determine the relative influence of, and interactions between, the forces shaping the zooplankton community as a

whole and to examine individual species-environment distributions in a set of shallow lakes. The homogeneity of lake type allowed the relative importance of physical, chemical and biological variables in dictating zooplankton community composition to be more fully explored than in previous studies.

2.2 Study area and sites

Sites were selected from a larger 'pilot' study data set of 80+ lakes (Sayer & Davidson, unpublished data) in the U.K. and from a large 100+ lake data set in Denmark (Jeppesen et al. unpublished data). Selection criteria included TP, macrophyte abundance, alkalinity and where available information on the fish community. The aim was that the selected shallow lakes should represent the longest available, most evenly distributed, 'complex' gradient of response to nutrient enrichment.

A total of 39 lakes were sampled for this study, 29 sites in Norfolk, United Kingdom (U.K) and 10 sites in Denmark (DK). The lakes are predominantly artificial, their origins including flooded medieval peat pits (the Norfolk Broads), ornamental 'estate' lakes, mill ponds, and duck decoys. The sites are small (0.4–22.5 ha) with an average depth of <3 m and experience only temporary thermal stratification in very stable warm periods. Further details on the morphometric, physical, chemical and biological characteristics of the sites can be found in Chapter 1. Table 2-1 provides a summary of the salient physical, chemical and biological characteristics germane to this investigation.

2.3 Methods

The sites were visited at monthly intervals from April to October in 1999 (U.K) and 2003 (DK). Analysis of the water chemistry was undertaken each month, zooplankton was sampled monthly, and aquatic macrophytes were surveyed in June and August. Fish population surveys were carried once in late summer (August-September).

2.3.1 Water Chemistry

Water samples were collected, using a boat, from approximately the centre of each lake, 30 cm below the surface, in acid washed polyethylene bottles. Conductivity, pH and dissolved oxygen content (DO) were measured in the field using pre-calibrated meters. Total alkalinity was determined using a Hach field titration kit. Secchi depth (SD) was measured using a Secchi disc at the deepest point of the lake. Where the disc was visible on the sediment surface, the readings were adjusted, to provide an improved estimate, by reference to chlorophyll-*a* (Chla) values for U.K. sites and by calibration against light penetration data using a LI-COR LI-250 light meter in DK. Samples were filtered using GF/C filter papers for soluble reactive phosphorus (SRP) and nitrate nitrogen (NO_3^--N) which were determined using standard methods (APHA 1990). Filter papers were retained for Chla analysis, which was determined spectrophotometrically after acetone (U.K.) and ethanol (DK) extraction (Jepersen & Christoffersen 1987). Unfiltered samples were collected for TP determined by microwave digestion using the method described by Johnes & Heathwaite (1992).

2.3.2 Biological sampling

Zooplankton was sampled monthly between April and October, although data presented here are from August only. At this time macrophyte growth tends to be high and, newly spawned, or young of the year, fish predation is at or near its greatest (Jeppesen et al. 2003b). The population was sampled in the two main habitat types, central lake, referred to as open water (OW) and the lake edge (L). In shallow lakes where plants can potentially colonise the entire lake bed, the 'open water' may in fact contain extensive growth of macrophytes as well as areas of clear water. In this area a 2.5 m plastic tube (internal diameter ≈7.5 cm) was used to take a sample of the entire water column. Five tube samples were taken along a visual transect from the centre of the lake towards the margins. Samples were then pooled and filtered through a 50 μm net. Tube samples were taken both within and without macrophyte beds, depending on their occurrence along the visual transect. At the lake edge two metre trawls were carried out in three distinct locations, representative of the lake margin. A 50 μm net fixed to the end of a telescopic pole was used for sampling, thereby allowing access to the lake edge without disturbing the area. The three samples were subsequently pooled. All samples were narcotised using chloroform and then preserved in 40%+ iso-propanol.

Zooplankters were counted using a Sedgewick-Rafter counting cell on a compound microscope at x40–100 magnification. A minimum of 100 of the dominant species was counted from a sub-sample of known volume. Cladocera were identified with reference to Flössner (1972) and Alonso (1996). All individuals were identified to species where possible. Species-level identification for some Daphnids proved difficult and the guild of *Daphnia hyalina* agg. was used for species in that group. *Ceriodaphnia* species were placed in one group. Cyclopoid crustaceans were assigned to family: Calanoid or Cyclopoid.

Aquatic macrophytes were sampled in June and August 1999 (U.K) and 2003 (DK). The percentage volume infestation (Canfield et al. 1984) method was used to quantify macrophyte abundance. Plants were surveyed from a boat using a combination of grapnel, bathyscope and snorkelling depending on water depth and clarity. A large number of points (>30) were sampled in each lake. At each point water depth, mean plant height and percentage cover were measured for a notional area of 1 m^2 and point PVI calculated using the following formula

$$PVI = \frac{C \times M}{D}$$

Where C is percentage coverage of macrophytes, M is the mean height of macrophytes and D is water depth.

The mean of the point PVI, therefore, provided an estimate of the proportion of the water column occupied by plants and provided a whole-lake macrophyte percentage volume infested (PVI).

Fish point-abundance sampling by electrofishing (PASE) (Perrow et al. 1996, Skov & Berg 1999) was used to sample fish populations in August-September 1999 (U.K) and August 2003 (DK). This technique has been shown to be particularly effective in sampling the dominant small fish (<10 cm) of vegetated shallow lakes, whilst still sampling larger individuals (Perrow et al. 1996). Sampling was conducted in both lake edge and open-water habitats from a 3 m fibreglass boat using high frequency (600Hz) pulsed DC (rectangular wave at 300V with a variable duty cycle of 0-50%) electrofishing equipment (Electracatch WFC11-12 volt).

In the open-water zone, the boat was rowed systematically along imaginary transect lines covering the whole lake, whereas in the littoral zone, the boat was rowed around the entire perimeter. Points were taken every 6-10 oar strokes depending on the size of the lake. At each point, the anode was immersed rapidly through the water column to the lake bed and back to the surface, over a period of around 5 seconds. All stunned fish were captured by a long-handled (2 m), fine-meshed (5 mm) net and transferred to a bin of water within the boat to recover, before being identified and measured to the nearest mm fork length.

Estimates of the density by number (ind. m^{-2}) of each species were calculated for both open-water and littoral, or marginal, habitats (number captured / number of points / effective sampling area). These were combined to provide an overall estimate for the lake by determining the relative area of the littoral margin, or lake edge to the open water zone and weighting the densities accordingly. The total area of the marginal zone was estimated by multiplying an average width of margin, from estimates at each point, by length determined using a GIS. The area of the OW zone was thus calculated as the total lake area minus the marginal zone area.

Almost all fish species undergo some form of ontogenetic niche shift. Of particular importance in shallow lakes is the shift of perch from zooplanktivores via insectivore to piscivore (Persson et al. 1991). Fish data were divided into feeding guilds based on a combination of species and size. Bream below 90 mm, perch below 90 mm, all roach, all rudd, ruffe below 90 mm and all sticklebacks were categorised as zooplanktivores (ZF). Perch as small as 25 mm may display some piscivory of other 0+ fish (Beeck et al. 2002). Here, perch above 90 mm, eel and pike were termed piscivorous (PF) (Lundevall et al. 1999, Perrow et al. 1999). Bream above 90 mm, all carp and ruffe (*Gymnocephalus cernus* L.) above 90 mm were classified as benthivorous (BF). Tench were treated separately, because although they may be classified as benthivorous, their feeding behaviour and association with plants mark them out as different from bream and carp. No site with tench contained either bream or carp.

2.3.3 Data sets

There are a number of different zooplankton data sets presented here. As zooplankton display some horizontal variability in distribution (Jackobsen & Johansen 1987) two methods were employed in order to obviate any bias induced from using one method. The method employed in the lake margins was multiple net sweeps. As such, it is a semi-quantitative method, precluding the harmonisation of the OW and L counts into one whole lake abundance score. As a result the OW and L abundance data sets were analysed separately. The two data sets were, however, combined to create an estimate of whole lake percentage relative abundance of zooplankton taxa. This was achieved by converting the OW and L abundances to proportions, then weighting them by the area of the lake occupied by each habitat and summed to create a whole lake (WL) relative abundance for each species. The first few instars of both types of copepods were excluded prior to converting the abundances to percentages as they numerically dominated some sites.

The selection of environmental variables from the most appropriate time period was given careful consideration. It could be argued that summer mean values would better summarise the overall lake trophy, whereas the August sample may more accurately reflect late summer conditions. Most zooplankton species can reproduce parthenogenically and as such they can respond very quickly to a changing environment (Fryer 1993, Wetzel 2001). Choosing between samples was a trade-off between safety of a mean and the appositeness of the monthly sample. Notwithstanding the dangers of using one spot sample, August values were used for TP, SRP, Chla, Nitrate, EC, pH, Alkalinity and DO. August values were compared with the summer mean and the ranking of the sites was very similar for key variables such as Chla and TP (Appendix 1). August PVI, rather than average summer PVI was used as this may be a better reflection of the conditions the zooplankton were experiencing at the time. Several of the sites experienced a "crash" in vegetation cover between June and August, and a mean of the two periods would be unrepresentative. The impact of the high PVI in June at these sites would have disappeared by the time the August samples were collected. Fish were divided into feeding guilds as described above and two permutations were used for some of the regression analysis whereby bream <100 mm were reclassified as benthivorous rather than zooplanktivorous and labelled zooplanktivorous fish BB. A total of 15 environmental variables (Conductivity, pH, Alkalinity, TP, SRP, Chla, Nitrate, surface dissolved oxygen, bottom dissolved oxygen,

Secchi depth, Macrophyte PVI, ZF, BF, PF and Tench) were used in the analysis and are summarised in Table 2-1.

2.3.4 Numerical methods

A variety of numerical techniques were employed to explore the chemical and biological data presented here. Ordination was selected as an appropriate technique owing to its efficacy in investigating the patterns and causes of variation in large data sets (ter Braak & Prentice 1988). A combination of detrended correspondence analysis (DCA) (Hill 1973, Hill & Gauch 1980) constrained ordination, canonical correspondence analysis (CCA) (ter Braak 1986, 1987, 1994) and partial constrained ordination (partial CCA) (Borcard et al. 1992) were employed. The OW and L abundance data were log (x+1) transformed and the WL relative abundance (%) were square-root transformed. Environmental data were either log, log (x+1) or square-root transformed dependent on which transformation best approximated a normal distribution. In the exploratory DCA rare taxa were down-weighted and detrending was carried out by segments. Ordination analyses were carried out using CANOCO version 4.5 (ter Braak & Smilauer 2002)

CCA provides a means of exploring community and environmental data simultaneously, providing useful information about the correlations between species abundance and environmental data (ter Braak & Verdonschot 1995). These methods, however, operate under the implicit assumption that all species share a common response model (ter Braak 1986). Additionally, the selection of CCA or RDA involves a choice between linear or non-linear community response to the strongest latent variable within the species data. This inevitably leads to a compromise, particularly when the length of the first gradient in the DCA falls between the two stools of linear and non-linear techniques with SD units between 1.5-3 (ter Braak 1986). In contrast, Generalised Linear Models (GLMs) (McCullaugh & Nelder 1987) allow both linear and non-linear response to environmental variables to be included in a single model. They were employed here to explore individual species' response to the environmental gradient in the 'training set' and to examine the veracity of the results from the constrained ordination analyses. A combination of GLM and CCA has proved effective in modelling species distribution (Hill 1991) each having distinct advantages and drawbacks (Guisan et al. 1999).

Modelling species abundance data containing many zeros and with a large amount of variance, in particular where the variance does not vary as a function of the mean (heteroscedasticity), is problematic. Traditional least-squares regression techniques are sub-optimal even when both predictor and response variables are transformed. The zooplankton abundance data presented here were not homoscedastic and were zero inflated, i.e. the data contain more zeros than would be predicted by the standard error models within GLMs (McCullaugh & Nelder 1987, Barry & Welsh 2002). As such, even maximum likelihood (ML) based regression techniques suffered problems, principally over-dispersion, when applied to these data. In order to obviate the problems of inappropriate error structure (Welsh et al. 1996) and to allow all species to be analysed by the same method, the abundance data were reduced to species presence/absence and logistic regression with a binomial error distribution was used. All regression analysis was conducted using R version 2.0.0. (The R Foundation 2004).

Logistic regression finds the best explanation for the response (y) variable from a linear combination of the explanatory (x) variable(s) (Crawley 2002). The scale of the species response depends on the scale of the predictors through a simple parametric function, called a link function. In this case the logit link function maps the 'real' scale of the response variable onto a 0-1 likelihood of occurrence scale. Where p is the probability that a species occurs then the model fitted was:

$$\text{Log}\,(p/(1-p)) = \beta_0 + \beta_1 x_1 + (\beta_{11} x_1^2) + \beta_2 x_2 + \beta_3 x_3$$

where x_1, x_2 and x_3 are the environmental variable which combine to form the linear predictor, β_0, etc., are coefficients, β_0 is the intercept and $(\beta_{11} x_1^2)$ is the addition of a quadratic term to the equation for variable x_1.

The results of the CCA and species t-scores were used as an indication of the best likely predictor variables. Stepwise GLM using the Akaike's Information Criteria (AIC) identified variable(s) where the CCA gave little indication of the important predictor variable. Stepwise AIC was, however, only used as an indication as AIC can prove to be too liberal a test, not penalising a model sufficiently for the addition of parameters. The final model was arrived at by further exploration of the species' responses. The real power

of logistic regression lies in the simultaneous analysis of the effect of a number of environmental variables (ter Braak & Loonman 1986). Thus, it provided an ideal tool to investigate the multiple causality of a species' presence or absence.

All models are wrong (Crawley 2002), but in order to find the "least wrong" model a number of tests were applied. The measure of discrepancy between the stipulated model, and the saturated model (with all parameters added) in a GLM is called deviance. Deviance is described as -2 times the difference in the log likelihood between the stipulated model and a saturated model (Nelder & Wedderburn 1972). Deviance functions in a similar way to sum of squares (total, residual and error) in least-squares regression. The proportion of variance explained by a particular model was calculated by comparing the null deviance (a model where all variation from the mean is attributed to the error component of the model) with the residual deviance (where the variation associated with the stipulated parameters is ascribed to the systematic component of the model and the remaining variation to the error component) which gives the D^2 value (analogous to R^2). Model goodness of fit was evaluated by the reduction in residual deviance as a proportion of null deviance, changes in which follow the F-distribution. Thus, the significance of adding additional parameters to the model could be assessed (Crawley 2002). Final model selection was based on a pragmatic combination of a significant reduction in residual deviance, the related AIC and the less liberal BIC (Bayesian information criteria) (Schwarz 1978) tests.

2.4 Results

2.4.1 Physical, chemical and biological characteristics

The 39 sites were shallow, high alkalinity, medium conductivity lakes and ponds with a large variation in trophic state (Table 2-1, Fig. 2-1). The lakes in the data set occupied both of the "stable states" (*sensu* Scheffer et al. 1993) including clear-water sites, with low Chla, high SD, low TP, abundant plants and low ZF density, and turbid sites, with high TP, Chla, low SD, absence of plants and dominance by ZF. The data set did not, however, display bimodality in these values corresponding to one or the other states. The lakes provided, not

only a large range of these environmental variables, but also a well distributed gradient between the extreme values (Fig. 2-1)

2.4.2 Zooplankton data

The data sets consisted of 39 taxa in the OW, 36 in the L and 42 in the WL data set. The most ubiquitous group was cyclopoid copepods and the most common cladoceran was *B. longirostris*. Overall zooplankton density (not including rotifers) ranged from 28.14 to 1,624 ind. l^{-1} in the OW and between 73.03 and 109,000 ind. l^{-1} in the L (Appendix 2).

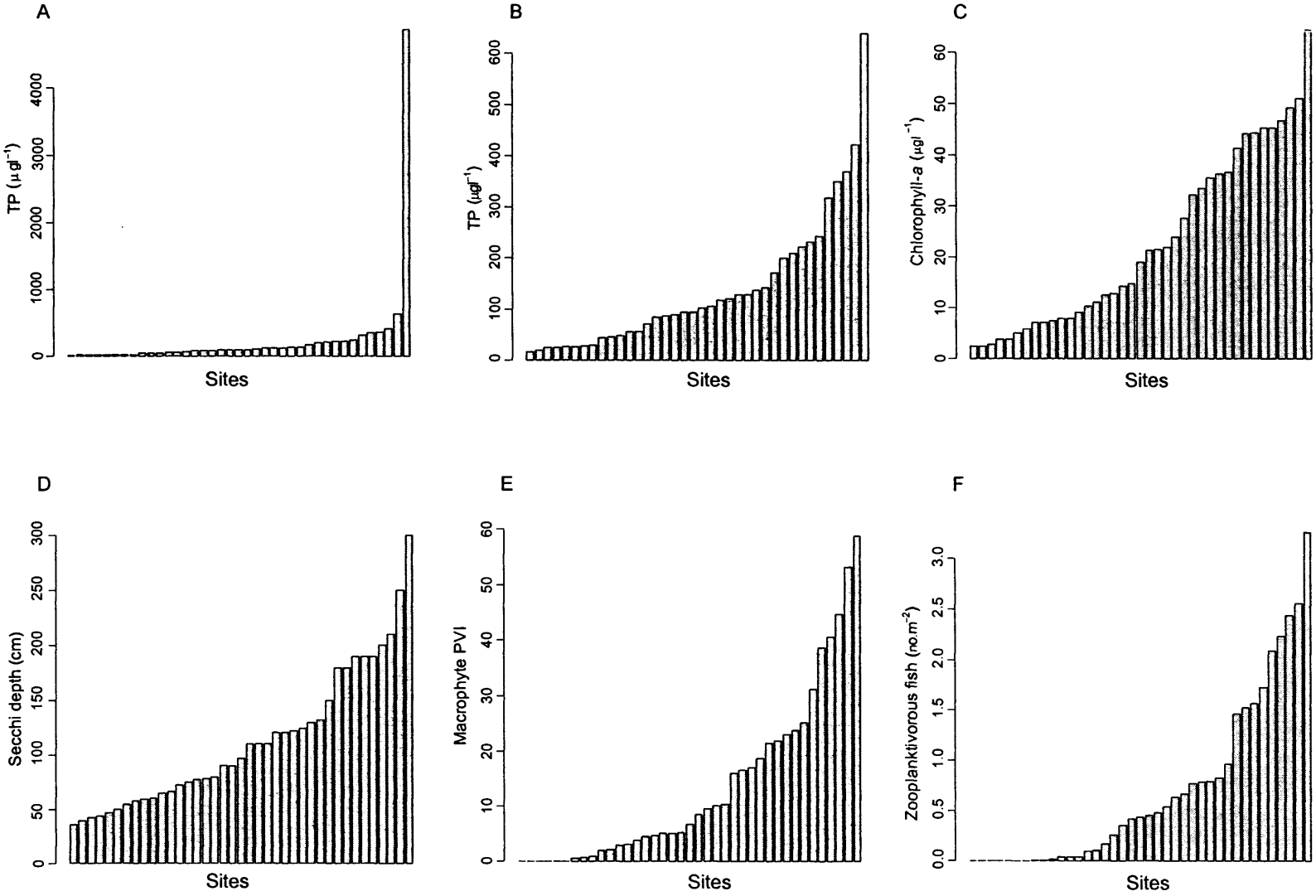
DCA results (Table 2-2) show the length of the first axis for OW and L lay in the range, between 1.5 and 3 standard deviation units, where both linear (PCA/RDA) and unimodal (CA/DCA/CCA) methods "can be used to good effect" (ter Braak & Prentice 1988). A data set with a gradient length, on its first axis of variation, which is less than two SD units has low variability within the data and linear methods (PCA and RDA) are deemed appropriate (Gauch 1982, Birks 1995). Where the first gradient length is greater than 2.5 SD the data set is assumed to be more heterogeneous and unimodal methods are recommended (Gauch 1982). Thus, for the OW and L samples both methods were appropriate, but for the WL data only CCA could be applied. In order to facilitate comparison of the different data sets non-linear methods (CCA) were used for all three data sets.

Table 2-1. Summary data for the 39 lakes for August: Conductivity (EC-μS cm^{-3}), pH, Alkalinity (Alk-mg $l^{-1}CaCO_3$), Total Phosphorus (TP-μg l^{-1}), Chlorophyll-*a* (Chla-μg l^{-1}), Soluble reactive phosphorus (SRP-μg l^{-1}), Nitrate (NO_3^--N mg l^{-1}), Surface dissolved oxygen (DO-%sat), Secchi depth (SD-cm), Macrophyte percentage volume infestation (PVI), Zooplanktivorous fish (ZF-fish m^{-2}).

Site code	Site name	EC	pH	Alk	TP	Chla	SRP	NO^-_3-N	DO	SD	PVI	ZF
BAYF	Bayfield Hall Lake	650	8.3	210	370	7.12	348	1.33	143	120	18.7	0.01
BEES	Beeston Hall Lake	580	7.5	162	200	19.01	28	0.43	74	120	25.2	0.54
BIGW	Big Wood Lake	650	8.5	175	137	50.91	22	1.36	257	75	8.5	0.84
BLIC	Blickling Hall Lake	420	9.8	48	118	45.38	3	0.04	186	42	0.9	0.26
BLUE	Bluestone Plantation Pond	470	8.1	120	29	12.75	2	0.02	110	190	21.5	2.24
BOND	Bonderup	411.6	8.0	160	17	10.29	2	0.01	85	250	44.7	2.56
BUCK	Buckenham Broad	580	8.5	198	142	41.37	22	0.44	110	97	10.4	1.53
BURF	Burntfen Broad	600	7.7	196	130	63.94	28	0.32	171	47	10.2	1.48
COSH	Cockshoot Broad	610	8.4	218	72	21.29	5	0.02	105	78	4.6	0.97
CROM	Cromes Broad	580	7.2	131	637	33.44	575	0.45	15	80	16	0.42
DECO	Decoy Broad	520	8.5	123	422	36.29	303	0.27	129	60	0	0.81
DEND	Denderup	394	7.7	182	86	5.83	36	0.01	68	190	23	0.00
DOJ	Døj Sø	387.2	8.3	124	95	35.57	4	0.01	132	90	5	0.05
ENSO	Ensø	348.5	8.5	104	121	24.02	34	0.01	107	55	0.5	0.37
FELB	Felbrigg Lake	490	8	119	172	14.88	45	0.32	102	58	0	2.44
GAMM	Gammlemose	391.3	9.4	116	130	46.69	32	0.01	190	40	3	0.18
GREP	Green Plantation Pond	540	7.5	90	24	2.89	100	0.22	73	300	21.9	0.00
GUB	Gub Sø	241	7.4	84	222	44.31	67	0.01	86	124	5	0.05
GUNT	Gunthorpe Hall Lake	460	7.3	175	56	44.12	7	0.18	87	122	17	1.58
HAVE	Haveringland Lake	520	8.5	102	84	36.60	3	1.37	214	36	0	3.26
HOKI	Holkham Hall Lake (Isolated)	520	7.8	137	44	3.90	30	0.86	107	200	2.1	0.00
HOKM	Holkham Hall Lake (Main)	440	8.5	138	102	14.36	15	0.84	60	73	0.8	0.00
LIST	Listrup lyng (Børresmose)	510	7.6	148	25	2.44	5	0.01	86	90	6.8	0.45
LOPO	Lowes Pond	495	7.9	186	26	8.07	23	2.13	100	180	0	0.80
LYLI	Lily Broad	620	7.7	190	232	5.17	207	0.06	67	132	2	0.12
MELT	Melton Constable	280	8.8	96	318	32.08	275	0.03	96	77	2.9	0.01
NARF	Narford Hall Lake	300	7.8	115	28	3.74	12	0.79	98	190	9.6	0.04

Site code	Site name	EC	pH	Alk	TP	Chla	SRP	NO^-_3-N	DO	SD	PVI	ZF
PEDH	Pedham Lake	460	7.3	131	350	45.38	202	0.92	99	50	3.8	0.68
SAHA	Saham Toney Mere	460	9	150	210	49.17	85	0.02	129	59	0	0.02
SALH	Salhouse Little Broad	590	7.8	195	90	22.06	55	0.92	110	110	31.2	0.65
SCOT	Scottow Pond	630	7.3	105	56	9.15	7	0.02	86	180	38.6	0.01
SELB	Selbrigg Pond	650	7.5	177	20	7.95	7	0.01	97	130	23.8	2.09
SORT	Sorte Sø	1051	7.8	366	4864	2.57	3899	0.01	38	65	0	0.00
STEN	Stensby	581	7.5	240	47	7.15	4	0.01	45	150	16.5	0.49
STRA	Stradsett Hall Lake	420	9	117	244	12.49	82	0.00	109	44	5.2	1.74
STRU	Strumpshaw Broad	1900	8.7	141	48	21.51	5	0.00	105	110	40.7	0.47
TRAN	Tranevig	304	7.5	66	94	27.62	12	0.01	63	110	58.8	0.77
UPTO	Upton Broad	350	9.2	100	26	7.43	5	0.00	171	66	53.2	0.11
WOLT	Wolterton Hall Lake	470	7.7	124	106	11.22	70	0.03	80	210	4.5	0.00
	Mean	**552.4**	**8.2**	**167.3**	**227.9**	**27.8**	**135.2**	**0.52**	**107**	**112**	**13.8**	**0.714**
	Minimum	**266.3**	**7.5**	**71.0**	**19.4**	**2.0**	**3**	**0.01**	**15**	**36**	**0**	**0.0**
	Maximum	**1378**	**9.0**	**366.0**	**4056**	**85**	**3065.8**	**2.6**	**257**	**300**	**58.8**	**3.26**

Figure 2-1. Range of key chemical and biological variable from August in the data set a) TP ($\mu g\ l^{-1}$), b) TP ($\mu g\ l^{-1}$), with one site with extremely high value (SORT) removed, c) Chlorophyll-*a* ($\mu g\ l^{-1}$), d) Secchi depth (cm), e) August PVI, f) Zooplanktivorous fish density (no. m^{-2}).



The summary DCA data (Table 2-2) highlights some of the differences between the data sets. The OW communities had greater species turnover along axis one than the L, suggesting that there was less difference in the L communities between sites. The WL relative abundance data set had the longest first axis gradient, the habitats combined having a larger number of species and more distinct communities at the opposite ends of the first axis. The second axis of the DCA on the L counts had a smaller eigenvalue compared to the other data sets, indicating that much like the first axis less variance was explained on the second axis compared with the OW communities.

Table 2-2. Summary of results from DCA of August cladocera data for the abundance data for the OW and L habitats and the WL weighted relative abundance

	DCA axis	1	2	3	4	Total inertia
OW abundance	Eigenvalue	0.345	0.265	0.119	0.057	1.705
	Gradient length	2.538	2.532	2.008	1.620	
L abundance	Eigenvalue	0.301	0.158	0.102	0.071	1.888
	Gradient length	2.381	2.233	1.75	2.015	
WL relative	Eigenvalue	0.425	0.242	0.105	0.054	2.110
abundance	Gradient length	3.112	2.401	1.591	1.628	

2.4.3 Constrained ordination and variance partitioning

The constrained ordinations (CCA) of the three data sets (Table 2-3) show that in all cases the fifteen variables explained just over half of the variance in the data sets. The distribution of species in ordination space in the biplot were most similar between the OW and WL analysis (Figs. 2-2 & 2-4), whereas the biplot of the L displayed a number of differences in the patterns of species distribution (Fig. 2-3).

The first ordination axis for the OW reflected a change from pelagic species, various *Daphnia* spp., *Diaptomus* spp. and *B. longirostris* varieties to benthic/epiphytic species and was correlated positively with PVI, EC and alkalinity and negatively with TP (Fig. 2-2). Axis two was characterised by a shift from large bodied *Daphnia* to the smaller *B. longirostris,* and was positively associated with ZF density and Chla and negatively with tench and secchi depth (SD). Some taxa fell towards the centre of the plot, e.g. the cyclopoid copepods, their juvenile stage, termed copepodites and *Ceriodaphnia* spp. Forward selection with a Bonferonni correction (Legendre & Fortin 1989), indicated that

ZF and PVI represented the minimal adequate model, the addition of further variables not significantly increasing the amount of variance explained by the canonical axes (Table 2-4).

Table 2-3. Summary CCA results for the cladocera data with the full set of 15 explanatory variables: TP, Chla, SRP, NO^-_3-N, Surface DO, Bottom DO, pH, Conductivity, SD, August PVI, Alkalinity, Zooplanktivorous fish, Benthivorous fish, Piscivorous fish and Tench.

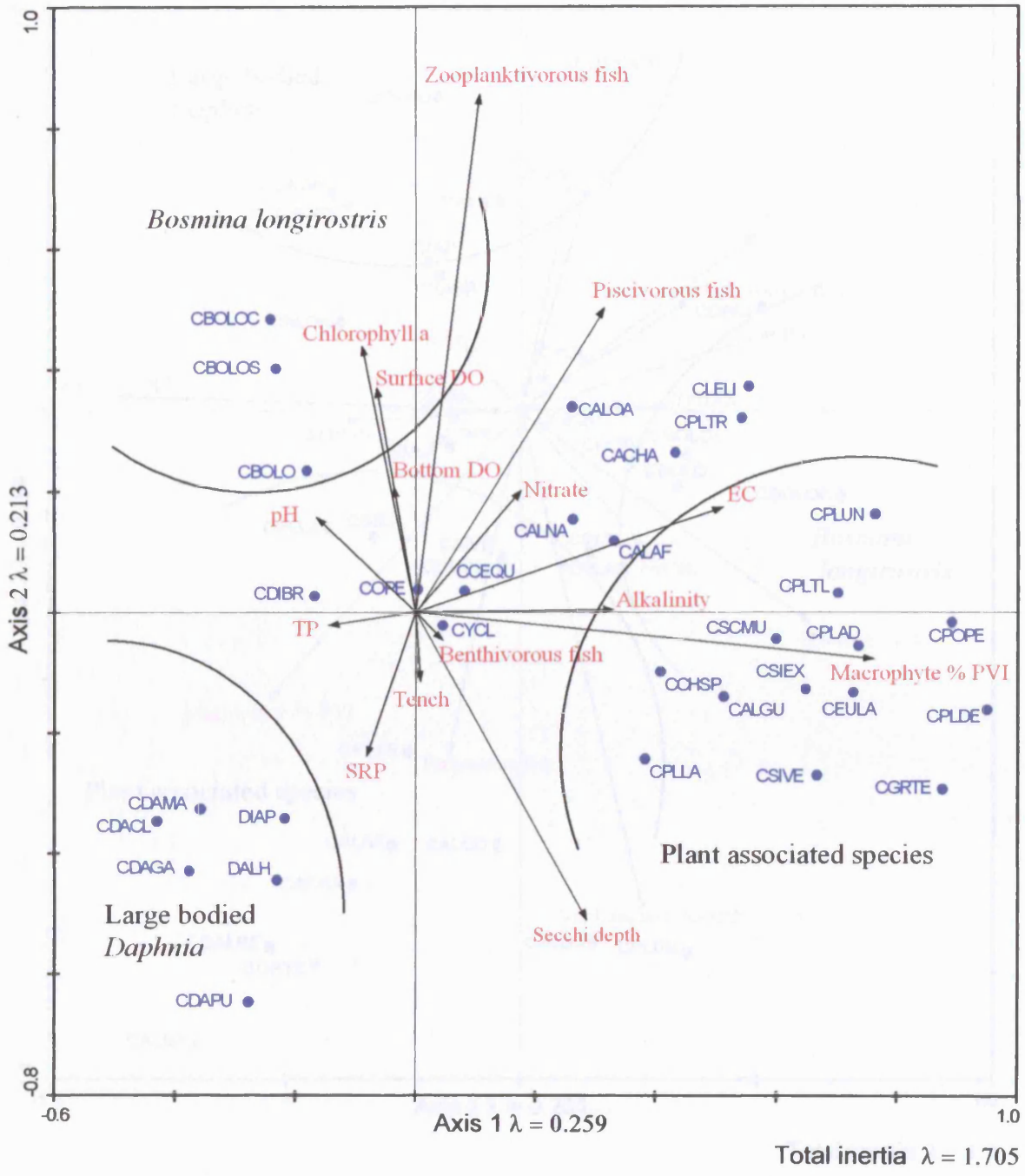
	CCA axis	1	2	3	4	Total inertia
OW abundance	Eigenvalues (λ)	0.259	0.213	0.096	0.074	1.705
	Cumulative % variance of species data	15.2	27.6	33.3	37.6	
	Cumulative % variance of species-environment relation	29.6	53.9	65.0	73.4	
	Sum of canonical eigenvalues					0.874
	% Variance explained					**51.3**
L abundance	Eigenvalues (λ)	0.231	0.194	0.109	0.085	1.900
	Cumulative % variance of species data	12.1	22.3	28.1	32.6	
	Cumulative % variance of species-environment relation	24.5	45.1	56.7	65.7	
	Sum of canonical eigenvalues					0.941
	% Variance explained					**49.5**
WL relative abundance	Eigenvalues (λ)	0.278	0.253	0.146	0.110	2.114
	Cumulative % variance of species data	13.2	25.1	32.0	37.2	
	Cumulative % variance of species-environment relation	26.0	49.7	63.3	73.5	
	Sum of canonical eigenvalues					1.070
	% Variance explained					**50.6**

The CCA of L abundance data displayed a marked difference in the patterns of species-environment association compared with the OW (Fig. 2-3). As in the OW, there was a general change from large to smaller pelagic species associated with an increase in ZF density and Chla, but also a strong negative association with SD. The grouping of the *Daphnia* spp. was much less tight, with *Daphnia cucullata* Sars, in particular, showing a marked difference in its location between the OW and L biplots. The separation of benthic/epiphytic species from pelagic species, whilst still identifiable, was also less marked. *Ceriodaphnia* spp. and *Cyclops* spp. again lay in the centre of the plot. The association of the different functional groups of cladocera to the driving environmental variables appeared less strong in the L samples, as reflected by the smaller proportion of variance attributable to the forward selected variables of SD and ZF (Table 2-4). SD explained the most variance (9.1%) in the zooplankton assemblage followed by ZF (6.6%) with a small co-variation term between the two parameters (0.4%) (Table 2-4). The WL

relative abundance CCA (Fig. 2-4) and partial CCA displayed similar patterns to the OW data. Bonferonni-corrected forward selection chose ZF and PVI as the minimum adequate model. There were again two main axes in the data, although they did not correlate with the ordinal axes. There was the marked shift from pelagic to epiphytic/benthic species concomitant with increasing PVI and a change from large to small-bodied species pelagic species with rising ZF density.

A notable feature of the environmental data set presented here was the fact that ZF density and PVI were orthogonal (Figs. 2-2, 2-3 & 2-4), meaning that lakes with low PVI had both high and low fish density and conversely high PVI sites had both high and low zooplanktivory. This lack of co-linearity facilitated the disentangling of the effects of PVI and ZF on zooplankton community composition and species distribution.

Figure 2-2. CCA of OW zooplankton abundance constrained by 15 environmental variables: TP, Chla, SRP, NO^-_3-N, Surface DO, Bottom DO, pH, Conductivity, Secchi depth, August plant abundance, Alkalinity, Zooplanktivorous fish, Benthivorous fish, Piscivorous fish and Tench.



Taxa are CACHA – *Acroperus harpae*; CALAF – *Alona affinis*; CALGU – *Alona guttata*; CALNA – *Alonella nana*; CALOA - *Alona* spp.; CBOLO – *Bosmina longirostris*; CBOLOC – *Bosmina longirostris var. cornuta*; CBOLOS - *Bosmina longirostris var. similis*; CCEQU – *Ceriodaphnia* spp.; CCHSP – *Chydorus sphaericus*; COPE – Copepodite; CYCL – Cyclops; CDACL - *Daphnia cucullata*; CDAGA – *Daphnia galeata*; DALH – *Daphnia longispina/hyalina*; CDAMA – *Daphnia magna*; CDAPU – *Daphnia pulex*; DIAP – *Diaptomus*; CDIBR – *Diaphanosoma brachyurum*; CEULA – *Eurycercus lamellatus*; CGRTE – *Graptoleberis testudinaria*; CLELI – *Leydigia leydigii*; CPLAD – *Pleuroxus aduncus*; CPLUN – *Pleuroxus uncinatus*; CPLDE – *Pleuroxus denticulatus*; CPLLA – *Pleuroxus laevis*; CPLTL – *Pleuroxus trigonellus*; CPLTR – *Pleuroxus truncatus*; CPOPE – *Polyphemus pediculus*; CSCMU – *Scapholeberis mucronata*; CSIEX – *Simocephalus expinosus* CSIVE – *Simocephalus vetulus*.

Figure 2-3. CCA of lake edge zooplankton abundance constrained by 15 environmental variables: TP, Cha, SRP, Nitrate, Surface DO, Bottom DO, pH, (EC), Secchi depth (cm), August macrophyte PVI, Alkalinity, Zooplanktivorous fish, Benthivorous fish, Piscivorous fish and Tench.

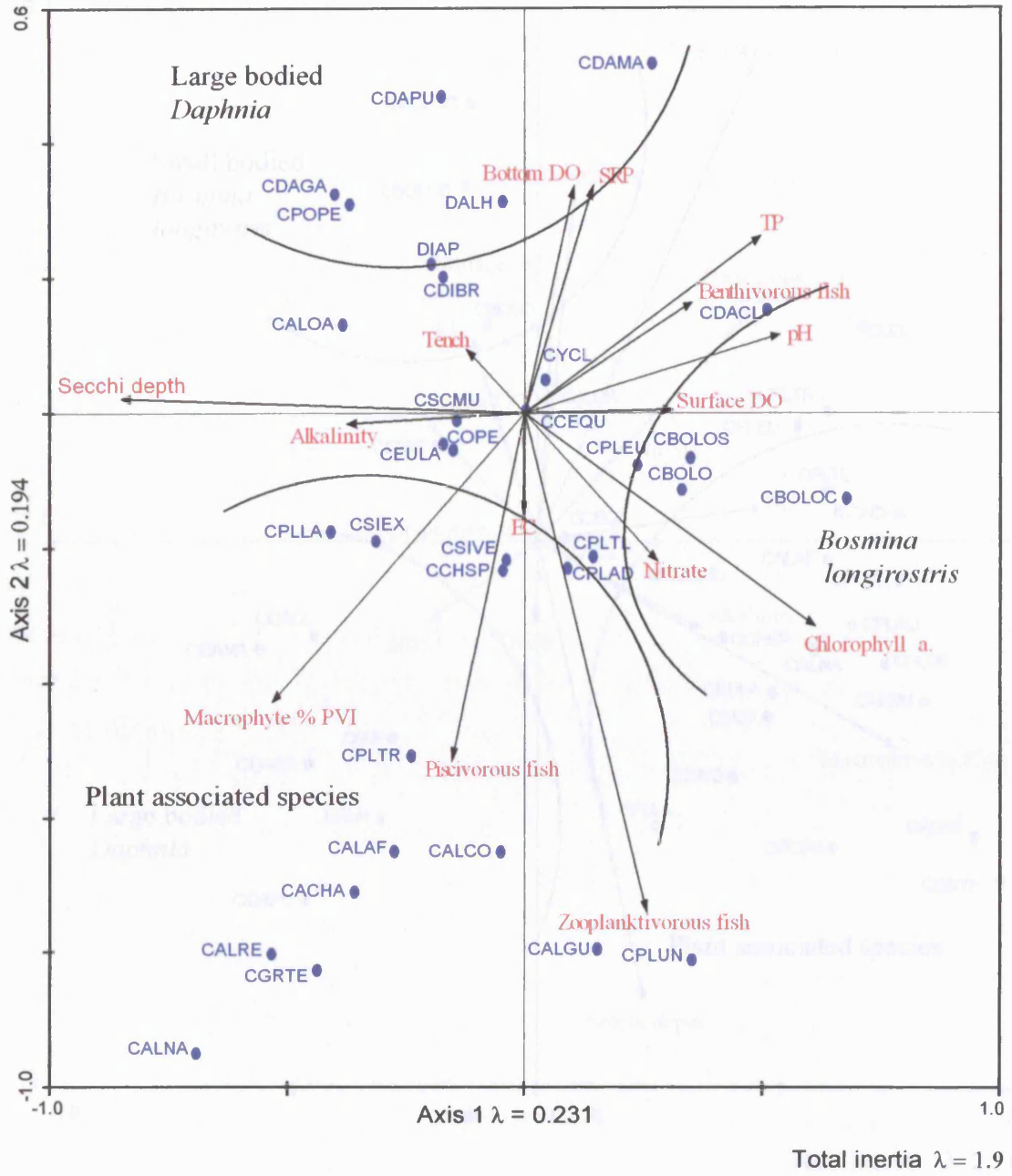


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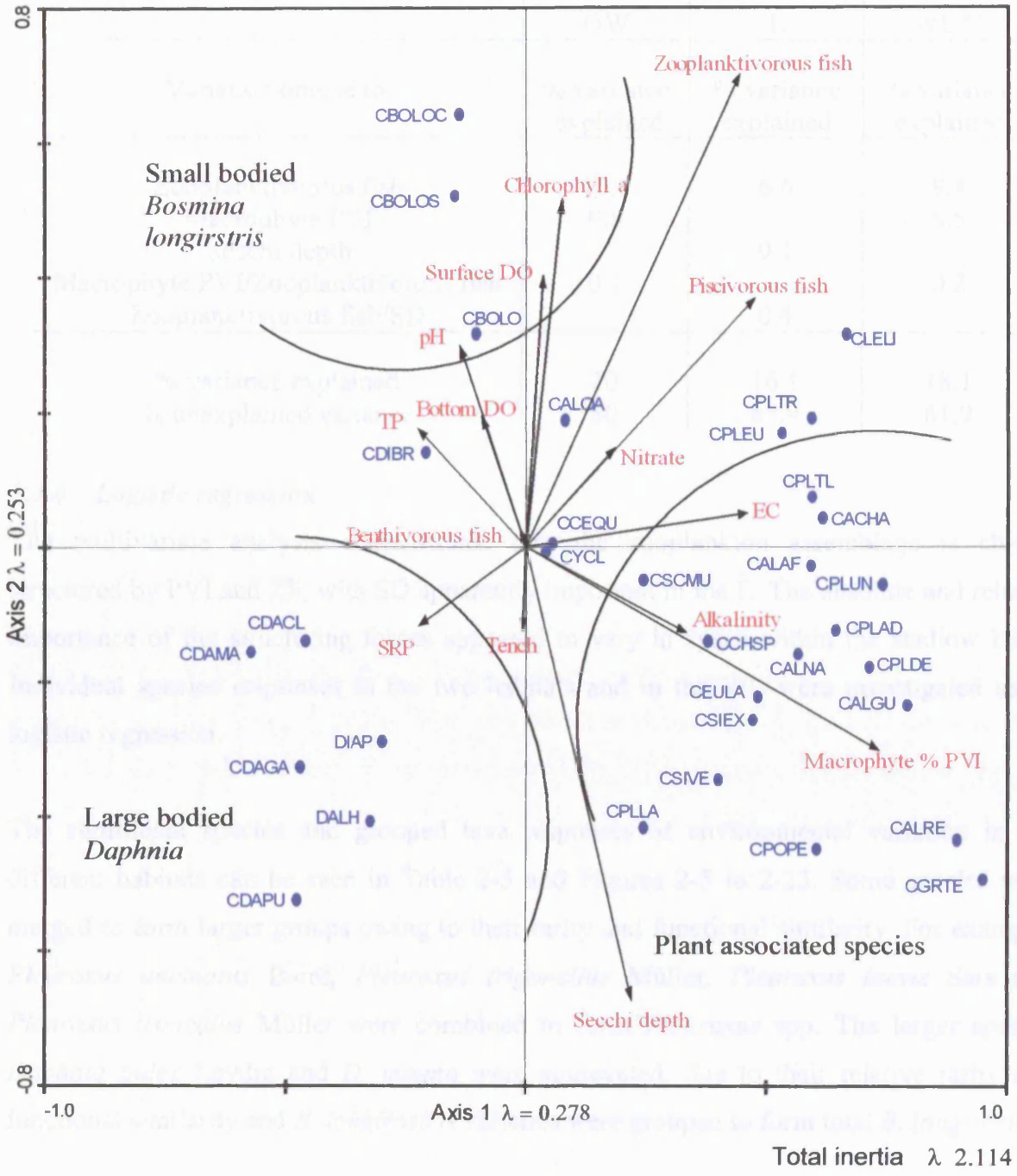
Figure 2-4. CCA of whole lake relative abundance constrained by 15 environmental variables: TP, Chla, SRP, Nitrate, Surface DO, Bottom DO, pH, EC, Secchi depth, Macrophyte PVI from August, Alkalinity, Zooplanktivorous fish, Benthivorous fish, Piscivorous fish and Tench.



Taxa are: (a) CACHA – *Acroperus harpae*; CALAF – *Alona affinis*; CALGU – *Alona guttata*; CALNA – *Alonella nana*; CALOA - *Alona* spp., CBOLO – *Bosmina longirostris*; CBOLOC – *Bosmina longirostris var. cornuta*; CBOLO - *Bosmina longirostris var. similis*; CCEQU – *Ceriodaphnia* spp.; CCHSP – *Chydorus sphaericus*; COPE – Copepodite; CYCL – Cyclops; CDACL - *Daphnia cucullata*; CDAGA – *Daphnia galeata*; DALH – *Daphnia longispina/hyalina*; CDAMA – *Daphnia magna*; CDAPU – *Daphnia pulex*,.; DIAP – *Diaptomus*; CDIBR – *Diaphanosoma brachyurum*; CEULA – *Eurycercus lamellatus*; CGRTE – *Graptoleberis testudinaria*; CLELI – *Leydigia leydigii*; CPLAD – *Pleuroxus aduncus*; CPLUN – *Pleuroxus uncinatus*; CPLDE – *Pleuroxus denticulatus*; CPLLA – *Pleuroxus laevis*; CPLST – *Pleuroxus striatus*; CPLTL – *Pleuroxus trigonellus*; CPLTR – *Pleuroxus truncatus*, CPOPE – *Polyphemus pediculus*; CSCMU – *Scapholeberis mucronata*; CSIEX – *Simocephalus expinosus*; CSIVE – *Simocephalus vetulus*.

Table 2-4. The explanatory power offered by each component and each co-variation term in the two component variance partitioning models for the three data sets from the 39 lakes.

	OW	L	WL %
Variation unique to:	% variance explained	% variance explained	% variance explained
Zooplanktivorous fish	10.1	6.6	9.4
Macrophyte PVI	9.8		8.5
Secchi depth		9.1	
Macrophyte PVI/Zooplanktivorous fish	0.1		0.2
Zooplanktivorous fish/SD		0.4	
% variance explained	20	16.1	18.1
% unexplained variance	80	83.9	81.9

2.4.4 Logistic regression

The multivariate analysis demonstrated that the zooplankton assemblage is chiefly structured by PVI and ZF, with SD apparently important in the L. The absolute and relative importance of the structuring forces appeared to vary in space within the shallow lakes. Individual species responses in the two habitats and in the WL were investigated using logistic regression.

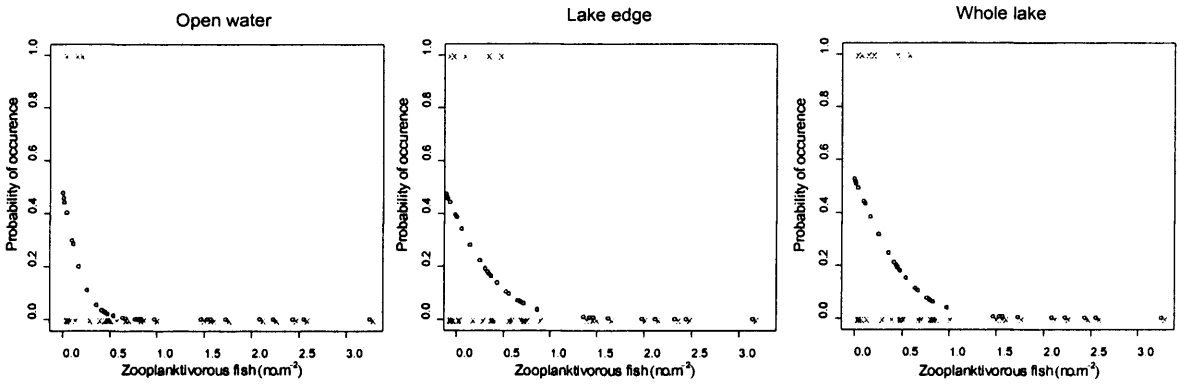
The significant species and grouped taxa responses of environmental variation in the different habitats can be seen in Table 2-5 and Figures 2-5 to 2-23. Some species were merged to form larger groups owing to their rarity and functional similarity. For example, *Pleuroxus uncinatus* Baird, *Pleuroxus trigonellus* Müller, *Pleuroxus laevis* Sars and *Pleuroxus truncatus* Müller were combined to form *Pleuroxus* spp. The larger species *Daphnia pulex* Leydig and *D. magna* were aggregated, due to their relative rarity and functional similarity and *B. longirostris* varieties were grouped to form total *B. longirostris*.

2.4.5 Pelagic species

The statistically significant models for pelagic species indicated that a variety of variables best predicted species occurrence and that responses were both linear and unimodal (Table 2-5, Fig. 2-5 to 2-14). *D. magna/pulex* displayed a dramatic decline as fish abundance increased (Fig. 2-5), the model suggesting they persist in the L at a slightly higher fish abundance than in the OW.

Note on logistic regression plot- X - In the lines plots denotes the presence (top) or absence (bottom) of the species at a that sites level of the particular variable in question. In the contour plots the X denotes the value of the variable for each site in the data set

Figure 2-5. Logistic regression modelling the probability of occurrence for combined *Daphnia magna* & *Daphnia pulex* predicted by zooplanktivorous fish density.



The next largest size guild *D. hyalina/longispina* displayed a complex non-linear response to PVI and a linear response to zooplanktivorous fish in the OW (Fig. 2-6 & 2-14). In the absence of plants, the likelihood of occurrence decreased sharply with increasing ZF, such that >1 ZF m^{-2} resulted in a predicted absence of *Daphnia*. The presence of plants, even at relatively low PVI, increased the probability of occurrence of *D. hyalina* agg. at ZF levels where they would be excluded in their absence. The model also indicated that once PVI increased above 30% there is a very low probability of occurrence for *D. hyalina* agg. In the absence of both plants and fish the model predicts a relatively small chance of *D. hyalina* agg. being present. In the L zone PVI had no discernible effect on the presence or absence of *D. hyalina* agg., which displayed a unimodal response to ZF with the likelihood of occurrence declining to a very low probability (Fig. 2-6) at around 1.5 m^{-2} then increasing at the highest ZF density. This increase was driven by two sites, Haveringland Lake (HAVE) and Stradsett Hall Lake (STRA), where *D. hyalina* agg. occurred in the L at a very high ZF density. At both these sites ZF was dominated by small bream. Bream is a shoaling fish species which avoids physical structures (Diehl 1988, Breukelaar et al. 1994) and may therefore tend to occupy the central area of the lake rather than the L. The reclassification of small bream as benthic resulted in a simple linear response, with >1 ZF m^{-2} resulting in the probable absence of *D. hyalina* agg. (Fig. 2-7).

Figure 2-6. Logistic regression modelling the probability of occurrence of *Daphnia hyalina* agg. predicted by macrophyte PVI and zooplanktivorous fish density in the OW and zooplanktivorous fish density alone for the L and WL.

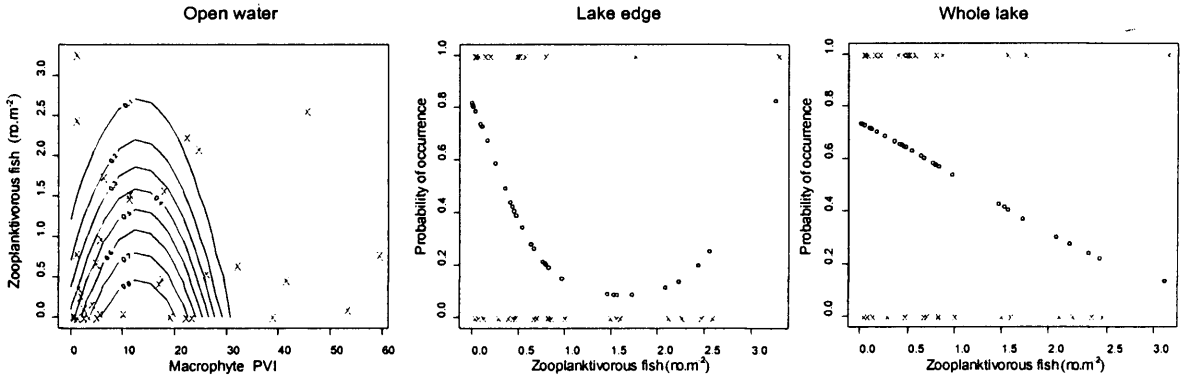


Figure 2-7. Logistic regression modelling the probability of occurrence of *Daphnia hyalina* agg. predicted by macrophyte PVI and zooplanktivorous fish density (BB, where bream <100 cm are classified as benthic) in the OW and zooplanktivorous fish density (BB) in the L and WL.

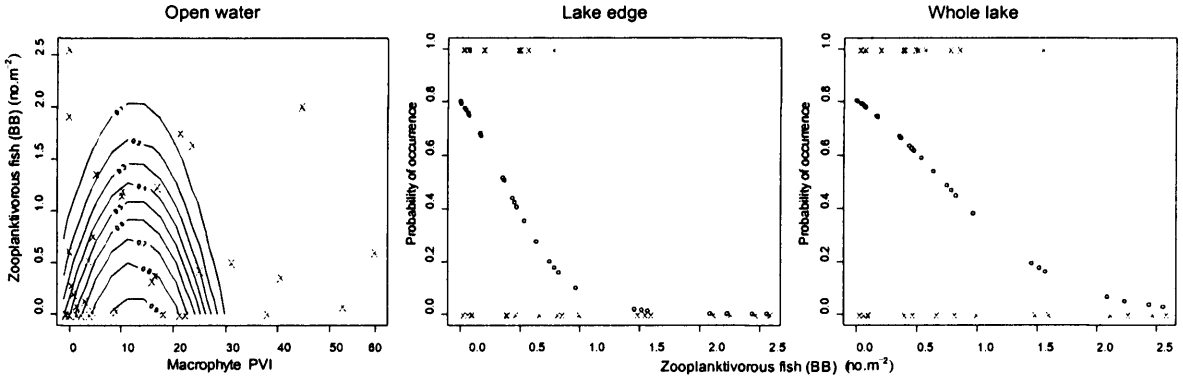
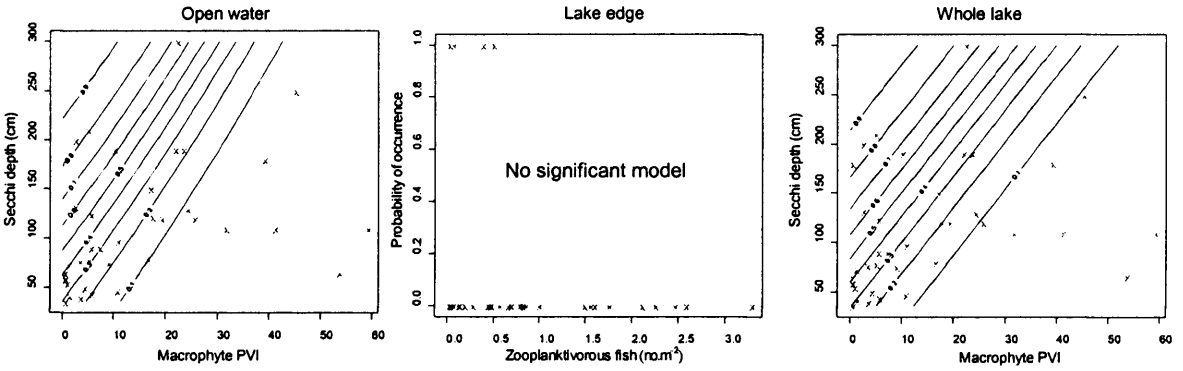


Figure 2-8. Logistic regression modelling the probability of occurrence of *Daphnia galeata* predicted by macrophyte PVI and secchi depth for OW and WL.



The occurrence of *Daphnia galeata* Sars in the OW and WL was best predicted by PVI and SD with its occurrence become increasingly likely as PVI fell and SD increased (Fig. 2-8). There was no significant model in the L.

The response of *D. cucullata* in the OW was a unimodal response to fish predation pressure (Fig. 2-9). This species was unlikely to occur in the complete absence of ZF but the likelihood rose at relatively low values of ZF (0.2-1 no. m^{-2}) and then declined again. The best predictor in the L was SD, *D. cucullata* occurring only where SD was low (Fig. 2-9).

Figure 2-9. Logistic regression modelling the probability of occurrence of *Daphnia cucullata* predicted by zooplanktivorous fish density in the OW and secchi depth in the L.

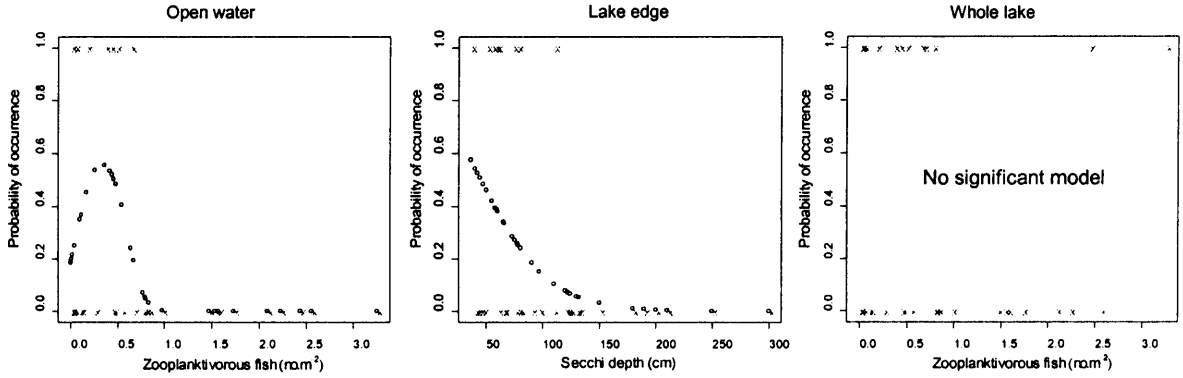
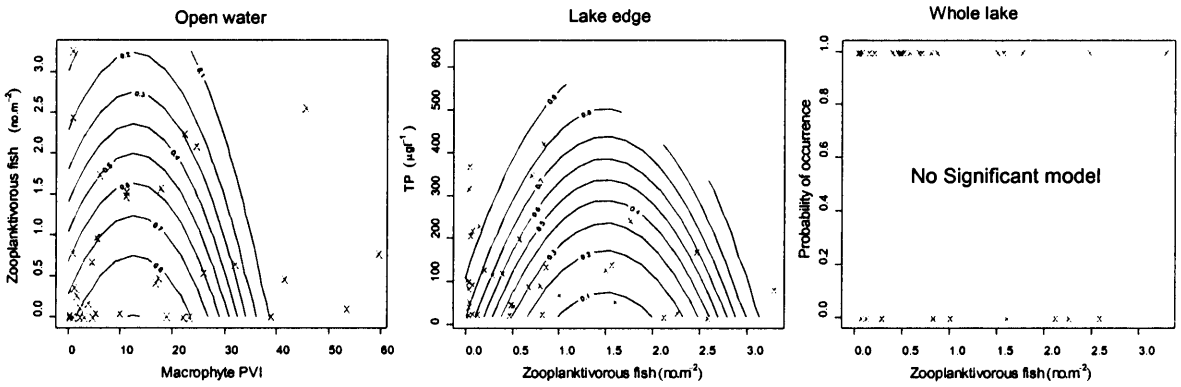


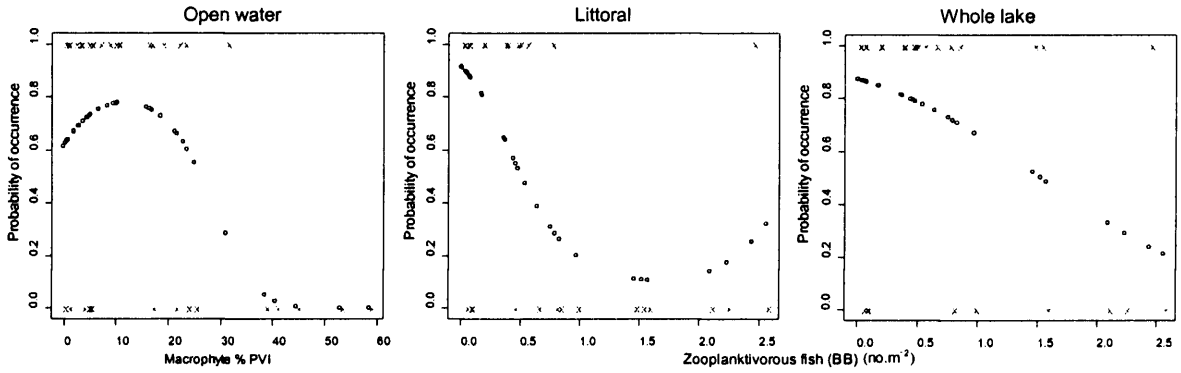
Figure 2-10. Logistic regression modelling the probability of occurrence of total *Daphnia* spp. predicted by macrophyte PVI and zooplanktivorous fish density in the OW and zooplanktivorous fish density and TP in the L.



The model of the combination of all *Daphnia* spp. in the OW (Fig. 2-10) displayed a unimodal response to PVI and a negative linear response to ZF density. At PVI >10% *Daphnia* persisted in the OW, even at relatively high ZF density, such that at PVI of 15% there remained a small likelihood of one of the *Daphnia* spp. persisting at even the highest fish density. At PVI >40%, even in the absence of fish, there was a very low likelihood of *Daphnia* occurring. In the L there was a unimodal response to ZF density and a linear response to TP (Fig. 2-10). The model predicted that the presence of *Daphnia* in the L was least likely at low TP and intermediate ZF density. When zooplanktivory fell and TP rose the probability of occurrence increased. There were, however, a lack of sites with high TP and high ZF, thus the model may be unreliable in this area. Where small bream were

reclassified as benthic (Fig. 2-11) the relationship between ZF and total *Daphnia* in the OW was no longer significant as the sites which actually have very high zooplanktivory in the OW, HAVE and STRA, contained a high proportion of small bream. There was still a unimodal relationship with ZF in the L though TP no longer significantly improved the model.

Figure 2-11. Logistic regression modelling the probability of occurrence of total *Daphnia* spp. predicted by macrophyte PVI in the OW and zooplanktivorous fish density (BB bream <100 cm classified as benthic) and in the L and WL.



The best predictor of the occurrence of *Ceriodaphnia* spp. was SD in all three data sets, but the addition of total *Daphnia* abundance, absolute or relative in the OW and WL respectively, and *D. cucullata* abundance in the L, further reduced the residual deviance of the model (Fig. 2-12). The high SD area of the models should be treated with caution as there were only two sites in this region, one with very high ZF Bonderup (BOND) and one with very low ZF Green Plantation Pond (GREP). Although ZF was not significant in the model, it clearly played an important role in determining the presence/absence and abundance of Daphnids. In the OW and WL the model predicted that as the abundance or relative contribution of *Daphnia* increased, the probability of *Ceriodaphnia* occurring decreased. In addition to this linear relationship there was a unimodal response to SD. At low and high SD the species was less likely to occur; at intermediate SD, there was still a low probability of *Ceriodaphnia* persisting even in the presence of a relatively dense population of *Daphnia* spp. In the L zone the best predictors of *Ceriodaphnia* occurrence were the abundance of *D. cucullata* and SD (Fig. 2-12). At very low SD the probability of occurrence rose in concert with *D. cucullata* abundance but as SD increased the association with *D. cucullata* disappeared and the probability of *Ceriodaphnia* occurring became more likely.

Figure 2-12. Logistic regression modelling the probability of occurrence of *Ceriodaphnia* spp. predicted by total *Daphnia* abundance and secchi depth in the OW and the WL and *D. cucullata* and secchi depth in the L.

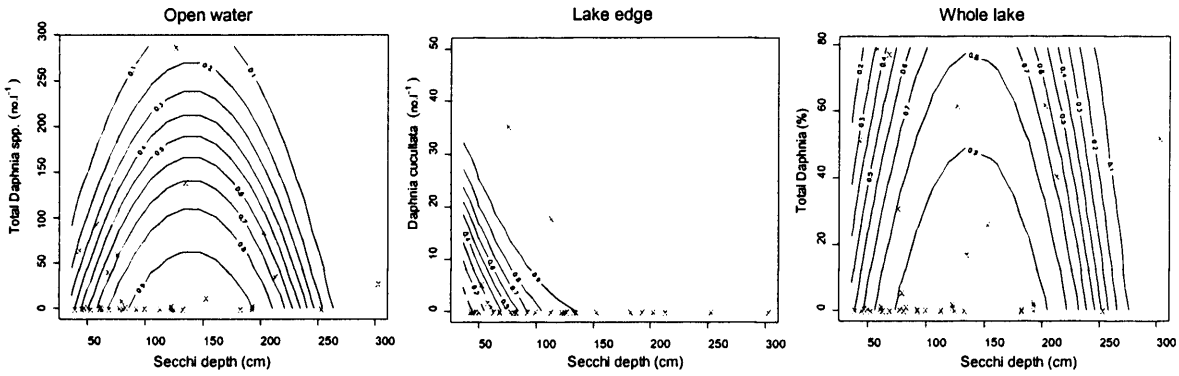
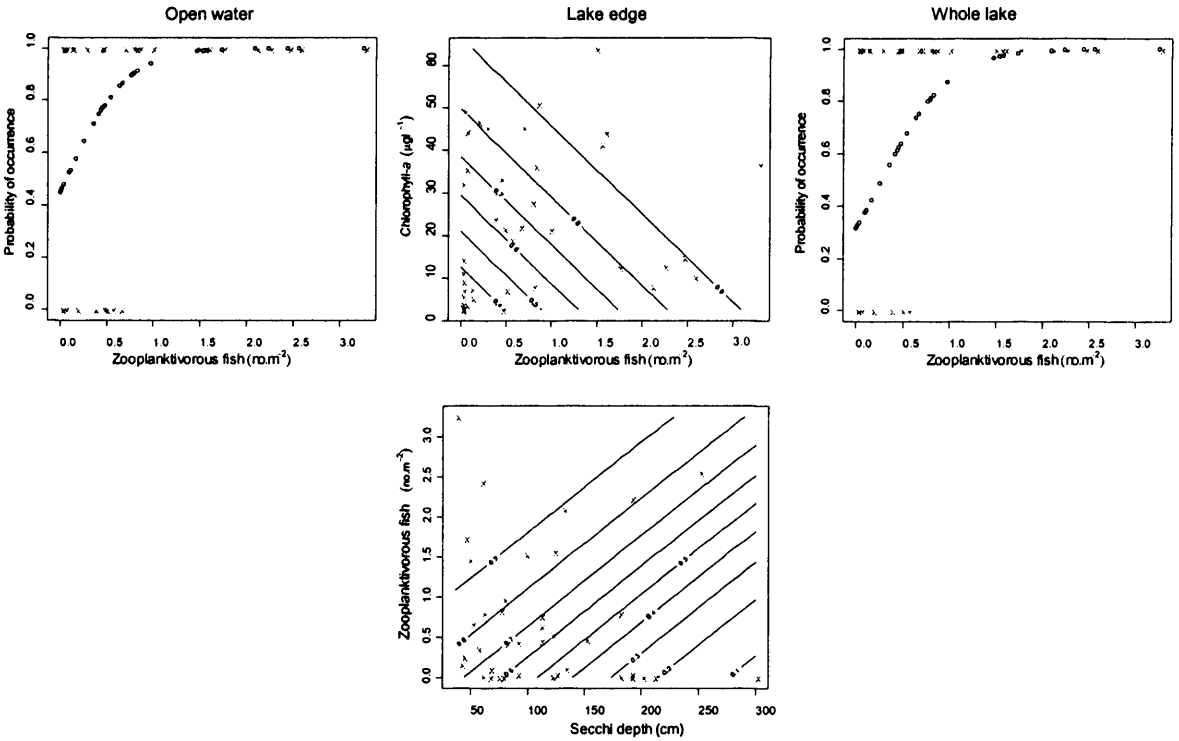


Figure 2-13. Logistic regression modelling the probability of occurrence of *Bosmina longirostris* predicted by zooplanktivorous fish density in the OW and the WL and predicted by zooplanktivorous fish density and Chla and zooplanktivorous fish density and secchi depth in the L.



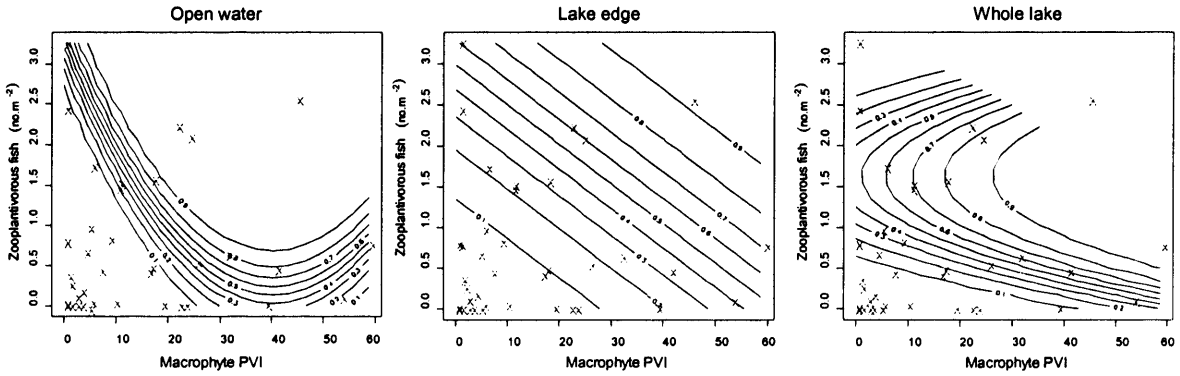
The likelihood of occurrence of *B. longirostris* was tightly linked to zooplanktivorous fish density (Fig.2-13) with a 100% likelihood of occurrence at fish densities $> \approx 1.0$ ZF m^{-2}. At the lake edge two models, one based on ZF and Chla, the other on ZF and SD had almost exactly the same diagnostics and criteria (BIC, AIC) scores. Both are presented (Fig. 2-13). The parity of the models was due to the strong negative correlation between Chla and SD (0.6). The species response was the same regardless of whether Chla or SD was used in

combination with ZF. At a given fish density, e.g. 1 ZF m^{-2}, Chla of <10 $\mu g\ l^{-1}$ results in a 50% likelihood of occurrence whereas at >50 $\mu g\ l^{-1}$ the likelihood of occurrence was >90%.

2.4.6 Benthic species

Acroperus harpae Baird (Fig. 2-14) displayed a relatively consistent response in both the OW and L habitats, apparently requiring plants to be present and becoming increasingly likely to occur as ZF density increased. In the WL analysis the likelihood of occurrence increased with PVI and there was a unimodal relationship with ZF, the likelihood of occurrence decreasing at low and high ZF density. The model was unreliable where both ZF and PVI values were large as the model was based on a limited population of sites (one) in that area. This has been termed the "curse of dimensionality" (Birks 1998), where the addition of parameters to the model exponentially increases the dimensions it is necessary to populate with sites in order for a robust model to be developed.

Figure 2-14. Logistic regression modelling the probability of occurrence of *Acroperus harpae* predicted by zooplanktivorous fish density and macrophyte PVI for all three data sets. In the WL plot the area of the model based on a limited number of sites is blocked out.



The *Alona* aggregate responded to plant abundance in the OW (Fig. 2-15) and WL data sets. In the L zone, however, there was a weak unimodal response to zooplanktivory, and a linear positive relationship with SD, the likelihood of occurrence of *Alona* spp. increasing in concert with SD (Fig. 2-15). *Alonella nana* Baird responded to plant PVI and ZF abundance with the highest likelihood of occurrence at intermediate PVI and high ZF for the WL. In the OW, however, the simplest model was based on TP (Fig. 2-16).

C. sphaericus showed a simple linear response to PVI (Fig. 2-17). The one site with very high PVI where *C. sphaericus* did not occur was Upton Broad (UPTO). Models for the large bodied *Eurycercus lamellatus* Müller and the smaller *Graptoleberis testudinaria*

Fischer indicated that both species responded to PVI (Figs. 2-18 & 2-19). Neither of these plant-associated species were recorded at the very high PVI site UPTO. This absence, along with the relatively small number of records for these species result in low D^2 values (Table 2-5), thus indicating a relatively poor fit to the model.

Figure 2-15. Logistic regression modelling the probability of occurrence of *Alona* spp. predicted by macrophyte PVI for OW and WL and for zooplanktivorous fish density and secchi depth in the L.

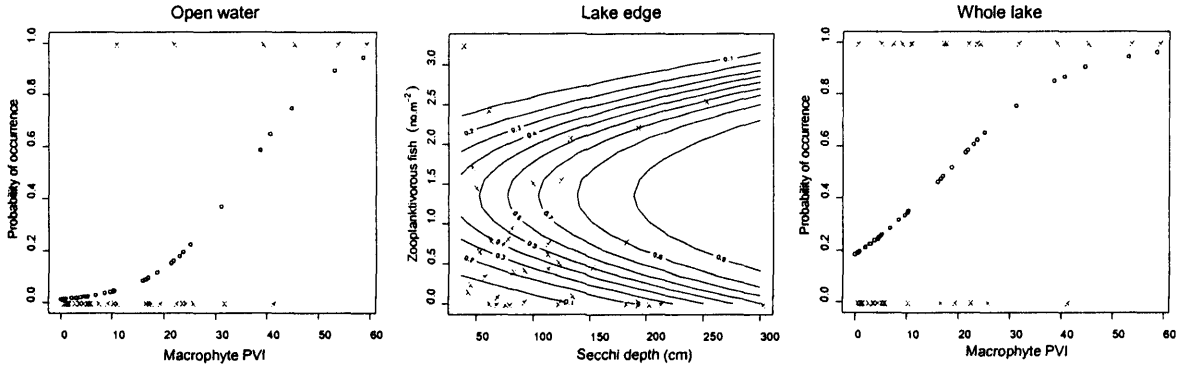


Figure 2-16. Logistic regression modelling the probability of occurrence of *Alonella nana* predicted by TP in the OW and zooplanktivorous fish density and macrophyte PVI for the WL. In the WL plot the area of the model based on a limited number of sites is blocked out.

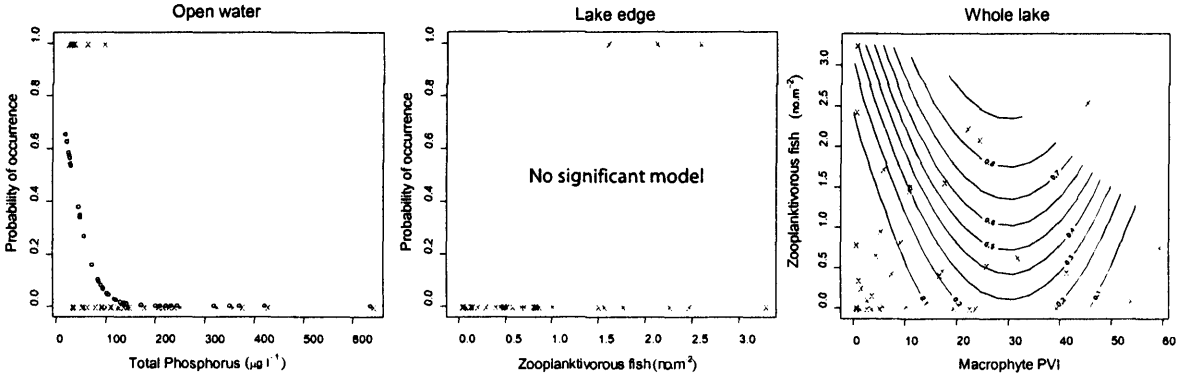


Figure 2-17. Logistic regression modelling the probability of occurrence of *Chydorus sphaericus* predicted by macrophyte PVI.

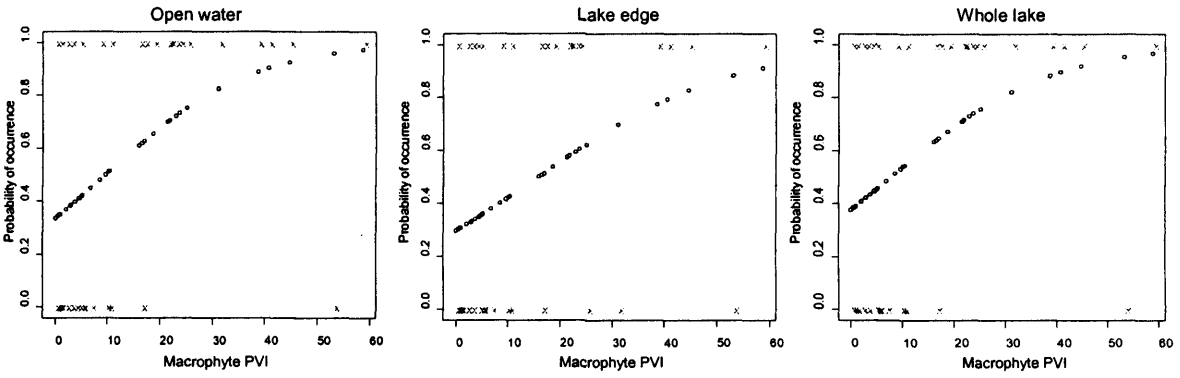


Figure 2-18. Logistic regression modelling the probability of occurrence of *Eurycercus lamellatus* predicted by macrophyte PVI in the OW and macrophyte PVI and secchi depth in the whole lake.

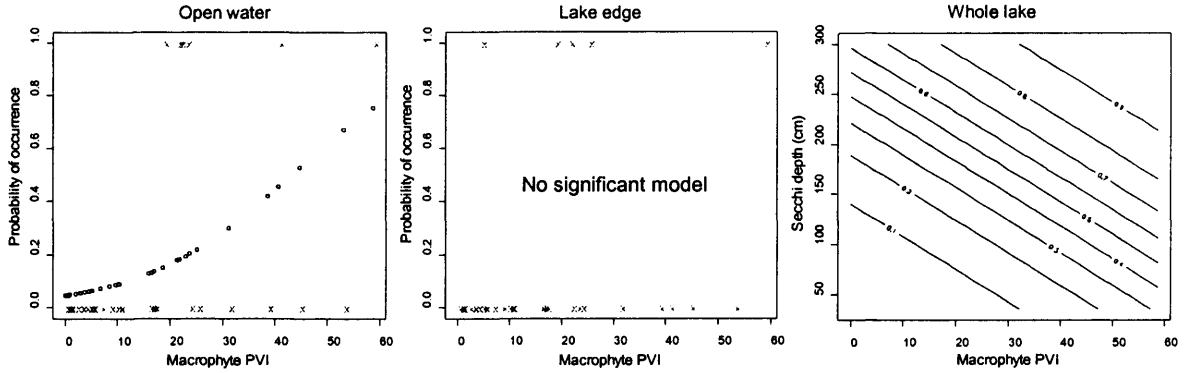
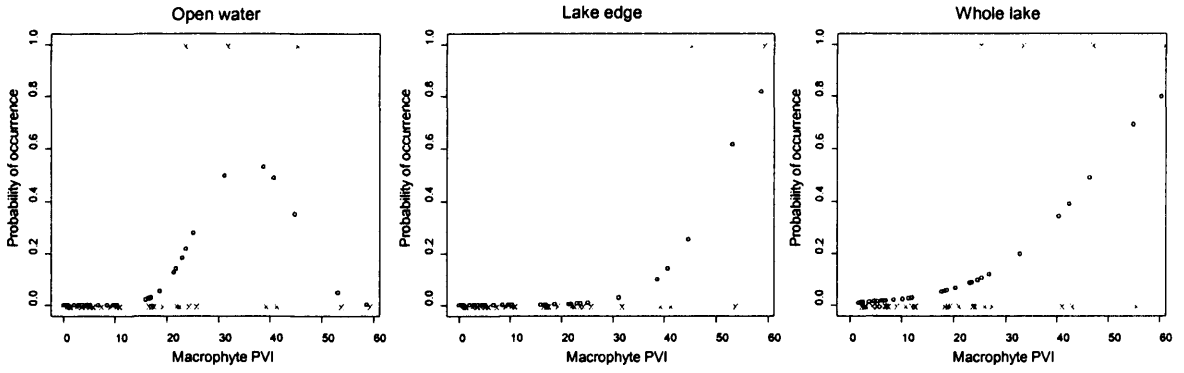


Figure 2-19. Logistic regression modelling the probability of occurrence of *Graptoleberis testudinaria* predicted by macrophyte PVI.



Pleuroxus aduncus Jurine was recorded at a sufficient number of sites for its distribution to be modelled separately, whereas the remaining *Pleuroxus* spp. were grouped because of their low occurrence (Fig. 2-20 & 2-21). The modelled distribution of *P. aduncus* predicted its most likely occurrence at intermediate macrophyte density with it becoming absent at very high PVI for both OW and L. The remaining species *P. laevis, P. trigonellus, P. truncatus* and *P. aduncus* together displayed the same distribution patterns in the OW and WL data, with a positive linear response to PVI and a unimodal response to ZF. *Pleuroxus* spp. was most likely to occur at high plant PVI and low to intermediate fish density. Where values of ZF and PVI were both low the likelihood of occurrence was very low. At a ZF density of around 1 fish m^{-2} *Pleuroxus* spp. occurred at a lower plant density when fish density was low. In the L zone there was a weak but significant unimodal response to ZF density (Fig. 2-21).

The occurrence of *Simocephalus* spp. consisting of *Simocephalus vetulus* Müller and *Simocephalus expinosus* DeGeer was best predicted by PVI. The OW and WL data

indicated a unimodal model, with the likelihood of occurrence falling at very high PVI. The L data had a positive linear association (Fig. 2-22). The unimodal response, however, was dependent on the species' absence from one site of relatively high PVI, UPTO. Thus, it may be that the species has a simple positive relationship with PVI, with some factor other than August PVI resulting in the rarity or absence of *Simocephalus* spp. at UPTO.

Figure 2-20. Logistic regression modelling the probability of occurrence of *Pleuroxus aduncus* predicted by macrophyte PVI.

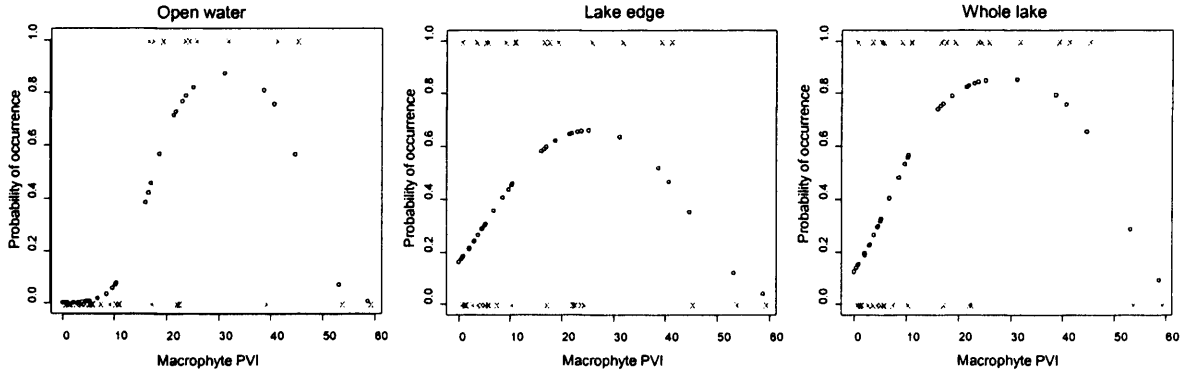


Figure 2-21. Logistic regression modelling the probability of occurrence of combined *Pleuroxus* spp. (*P. laevis, P. trigonellus, P. truncatus & P. uncinatus*) predicted by macrophyte PVI and zooplanktivorous fish density in the OW and WL and by zooplanktivorous fish density in the L.

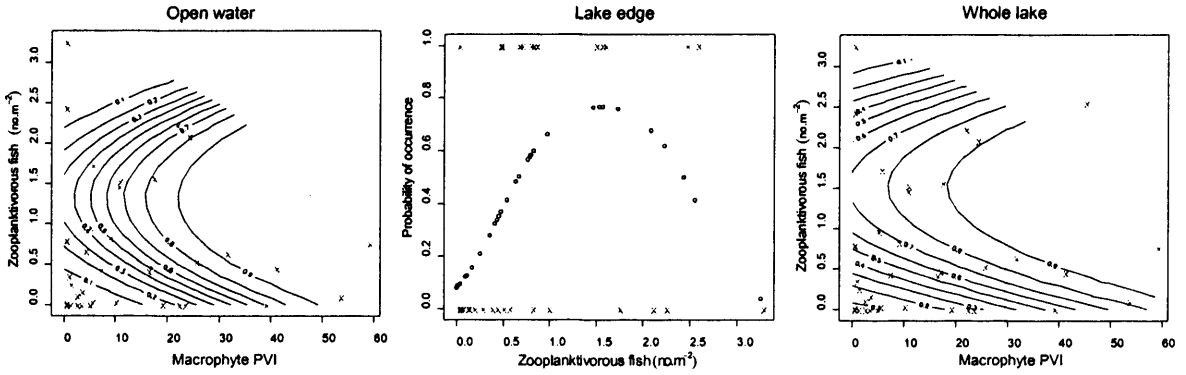


Figure 2-22. Logistic regression modelling the probability of occurrence of *Simocephalus* spp (*S. vetulus & S. expinosus* predicted by macrophyte PVI.

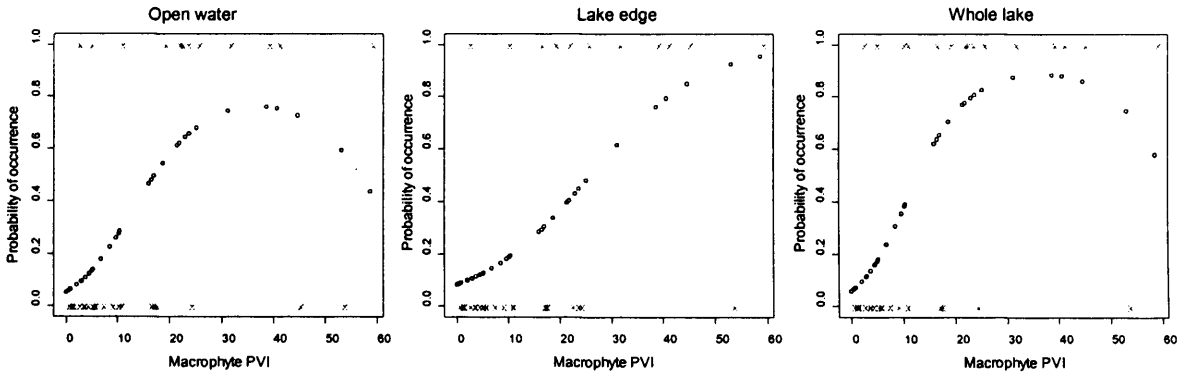


Table 2-5. Summary of the minimum adequate model and the statistical significance of the predictor variable(s) for species occurrence. M-macrophyte August PVI, Z-Zooplanktivorous fish, T-TP, D-Total *Daphnia* spp (no. l^{-1}), C- Chla, SD. ^2-indicates a quadratic term. sig- significance: *< 0.001; **< 0.01; *< 0.05; #< 0.1. NS, no significant model.**

	OW			L			WL		
Species	variable	sig	D^2	variable	sig	D^2	variable	Sig	D^2
Acroperus harpae	M^2 Z	** ** *	0.65	M Z	* **	0.31	M (Z^2)	* ** *	0.47
Alona spp.	M	** *	0.45	Z^2 SD	# *	0.22	M	**	0.20
Alonella nana	Z T	* ** *	0.37	NS			Z M^2	* *	0.37
Bosmina longirostris	Z	** *	0.25	Z C	* *	0.19	Z	** *	0.27
Ceriodaphnia spp.	D SD^2)	# **	0.30	D SD	* *	0.21	D SD	* *	0.30
Chydorus sphaericus	M	**	0.14	M	*	0.10	M	*	0.11
Daphnia cucullata	Z^2	*	0.23	SD	**	0.24	NS		
Daphnia galeata	M SD	* *	0.21	NS			M SD	 **	0.20
Daphnia longispina/hyalina	Z M^2	** *	0.31	Z Z^2	* **	0.26	Z	*	0.07
Daphnia lo/hy/pu/ma	M^2 Z	** **	0.32	Z Z^2	** **	0.32	Z	*	0.12
Daphnia magna & pulex	Z	** *	0.35	Z	**	0.23	Z	** *	0.25
Total *Daphnia* spp.	M^2 Z	** *	0.3	Z^2 TP	** *	0.34	NS		
Diaphanosoma brachyurum	NS			NS			D	**	0.15
Eurycercus lamellatus	M	**	0.21	NS (M-#)			M SD	* *	0.29
Graptoleberis testudinaria	M M^2	* *	0.44	M	***		M	**	0.38
Pleuroxus aduncus	M^2	** *	0.57	M^2	*	0.12	M^2	**	0.25
Total *Pleuroxus* spp.	M^2 Z	** *	0.53	Z^2	***	0.22	M Z^2	** * **	0.40
Scapholeberis mucronata	NS			NS			NS		
Simocephalus spp.	M^2	**	0.26	M	***	0.27	M^2	** *	0.34
Cyclops	NS			NS			NS		
Diaptomus	Z C T	* ** **	0.36	SD	**	0.16	C T	* **	0.33

2.5 Discussion

In accordance with previous work, the multivariate analyses and GLMs demonstrate that fish predation (Brooks & Dodson 1962, Schriver et al. 1995, Jeppesen et al. 2003b) and macrophyte abundance (Quade 1969, Whiteside 1970, Lauridsen et al. 1996, Stansfield et al. 1997) play key roles in structuring the zooplankton community of shallow lakes. Furthermore, water clarity is revealed as an important variable, particularly at the lake edge. Whilst SD may have some direct effects on the zooplankton community it is more likely that it best summarises what Whittaker et al. (1973) termed the 'complex gradient', where many linked parameters change in concert. The actual causative mechanism of change may be obscured by multiple causality, non-linearity of community response or variables associated with rather than responsible for any change. In the case of shallow lakes, increased SD is associated with *inter alia:* lower Chla, lower TP, the higher likelihood of abundant submerged macrophytes and lower ZF (Jeppesen et al. 2000). One diagnostic of this co-linearity of predictor variables is the variance inflation factors (VIF) produced in the CCA. TP, SRP and SD, respectively, had the highest VIF in all three CCAs indicating that SD had a high level of co-linearity with other explanatory variables. For a model to have any generality outside the data set it is based on, "it is desirable to predict the distribution of the biological entities on the basis of ecological parameters that are believed to be causal driving forces for their distribution and abundance" (Guisan & Zimmerman 2000). Thus, attributing causation of community change to SD should be done only where a likely mechanism is apparent.

The species response models suffer from the limitation that they are based on species presence/absence only. Thus, any information contained in the abundance data is lost. Additionally, often the best, or the least bad, model explains a relatively small amount of the variation in the data. Nevertheless, the species-specific models produced by logistic regression help shed some light on the patterns and perhaps even processes at work in shaping the zooplankton community. The modelling of likelihood of occurrence provides an indication of the conditions in which a species has a competitive advantage over another species, in other words its 'realised niche' (Hutchinson 1959). The niche concept states that there are two reasons why a species may not occur. Firstly, where the organism is excluded

by the environmental or physical conditions they are outside their fundamental niche (e.g. no water for an aquatic species, a lack of plants for an epiphytic species, or low pH for an acid-intolerant species). Secondly, where they are excluded by competition from other species, they are outside their realised niche. In most ecological gradients the majority of species appear to find one direction to be physically stressful (fundamental niche) and the other direction biologically stressful (realised niche) (Guisan & Zimmerman 2000). The physically stressful end of the gradient provides a relatively sharp boundary and therefore may be more likely to be consistent between sites. The biologically stressful end of the niche is dependent upon competition in turn related directly and indirectly to a number of factors and is much more likely to vary between sites. Thus, in terms of modelling species distribution and ecological preferences, or niches, the determination of the biologically stressful restriction of a species is likely to be far more problematic. The real power of logistic regression lies in the simultaneous analysis of the effect of a number of environmental variables (ter Braak & Looman 1986). It therefore, provided an appropriate tool to investigate the multiple nature of causality of species occurrences in environmental space. Particularly useful here was the ability to have a unimodal species response to one variable and a linear response to another. This is in contrast to ordination, which assumes either linear or unimodal species response, but allows abundance to be included in the model. Thus, the two types of analyses together provided complementary analyses (ter Braak & Prentice 1988, Guisan et al. 1999).

2.5.1 Pelagic species in the open water

The CCA and GLMs, for the OW data in particular, provided a multi-lake demonstration of the veracity and generality of the effects of size-selective predation by ZF (Brooks & Dodson 1962). The shift from large bodied (*Daphnids* and Calanoid copepods*)* to small bodied (Bosminids) taxa, via the intermediate sized *Ceriodaphnia* is concomitant with increasing zooplanktivorous fish density. The second major axis in the community data sets illustrates the importance of aquatic plants to zooplankton taxa such as *Simocephalus* spp., *Pleuroxus* spp. and *A. harpae*, with *Ceriodaphnia* spp. representing a 'halfway house' between pelagic and plant-associated species (Jeppesen et al. 2003a).

The regression analysis for the OW elucidated the resource partitioning of the different pelagic species and provided a large field-based endorsement of the 'size efficiency'

hypothesis (Brooks & Dodson 1962, Gliwicz 1990). The largest species *D. magna/pulex* proved the most efficient competitor in the absence of or at very low ZF. The lack of any association with PVI was perhaps illustrative of its disinclination to occupy plants as a source of refugia (Lauridsen & Lodge 1996). The smaller bodied species aggregate *D. hyalina* agg. displayed the greatest association with plants of all the *Daphnia* spp (Timms & Moss 1984). In accordance with a number of previous studies these data suggest *D. hyalina* agg. has a competitive advantage in the presence of fish with a PVI sufficient to provide some refuge from predation (Wright & Shapiro 1990, Schriver et al. 1995, Stansfield et al. 1997). In the absence of both ZF and PVI *D. hyalina* agg. was apparently out-competed by other *Daphnia* spp. The maximum likelihood of occurrence of *D. cucullata* in the OW indicated that the probability of its occurrence was highest once ZF attained a density sufficient to exclude *D. magna*. *D. cucullata* had no association with PVI, perhaps suggesting that once PVI rises smaller species are replaced by *D. hyalina* agg. The relatively small species *D. galeata* displayed an unusual distribution the model suggesting a preference for high SD and low plants. The response of the combined D*aphnia* species provided an illustration of the complexity species response with both ZF and PVI significant in determining its occurrence with a linear and unimodal response respectively.

The aggregated *Ceriodaphnia* spp. demonstrated no direct response to ZF in the open water. The modelled distribution of *Ceriodaphnia,* however, indicated that as *Daphnia* decreased in abundance *Ceriodaphnia* was most likely to occur (Fig. 2-12). The predictive power of SD in this relationship may be indirect as low water clarity is associated with high fish abundance, where *Ceriodaphnia* may be excluded through predation rather than competition from Daphnids. Similarly, despite the relationship not being statistically significant, the nuestonic species *Scapholeberis mucronata* Müller only occurs at low *Daphnia* abundances. As ZF levels increased even further, the occurrence of the smallest pelagic species, *B. longirostris*, in the open water became a certainty (Fig. 2-12). This provided a clear example of the realised niche, as in the absence of other species *B. longirostris* would occur at all sites, they were competitively excluded from sites with low ZF, and perhaps low TP, by larger bodied, more efficiently feeding species.

2.5.2 Pelagic species in the lake edge

The shift of importance of PVI to SD between the OW and L habitat indicates that macrophytes were less important for the community occupying the edge of the lake. The reduction in the total amount of variance explained by fish predation in L, as compared to the OW, suggested that the edge of lake communities were more similar between sites than the OW. It may be that the same species are found in the L at different sites but for different reasons. For example, in a lake with no plants and some ZF *Daphnia* spp. may persist in the margins of the lake but are absent in more pelagic areas (Jakobsen & Johnsen 1987). In contrast in lakes with plants and with a low ZF density, *Daphnia* spp. may occupy the edge of the lake, as in general, Daphnids avoid structure in the absence of ZF (Lauridsen & Lodge 1996). Thus, a 'less different' community may occur in the L as a result of the same structuring forces that established more distinct OW communities.

The regression analysis of the L indicates that the link between ZF and *Daphnia* was more ambiguous in the L than in the OW. Not all the *Daphnia* species displayed a direct response to ZF. Those that did (*D. magna/pulex, D. hyalina* agg.) persisted in the L at higher ZF densities than in the OW with the L apparently providing some form of refuge from ZF (Cryer & Townsend 1988). Whilst *D. galeata* displayed no significant relationship with ZF, it only occurred at relatively low ZF density. The lack of a significant relationship is a function of its absence from other sites with low fish density, indicative perhaps of competitive exclusion (biological stress) as well as the effects of predation (physical stress).

D. cucullata occurred in the L at sites with low water clarity irrespective of ZF. The model suggested that water clarity may be reduced to the point where a fish's 'reactive distance' was limited and the visual predator no longer encounter their prey frequently enough to restrict them (Gliwicz 2001). The same mechanism may be behind the unimodal response to ZF of *D. hyalina* agg. in the L, where the likelihood of occurrence declined to a minimum at 1.5 ZF m^{-2} and then increased at high ZF levels. This increase was driven by two sites where *D. hyalina* agg. occurs at high ZF. At both sites submerged vegetation was absent and water clarity was extremely low (SD of 36 and 44 cm, respectively). Furthermore, the zooplanktivorous fish population was dominated by small bream which tend to avoid physical structure (Moss et al. 1996a). In a shallow lake physical structure

consists largely of submerged macrophytes or in their absence the emergent plants and overhanging vegetation at the lake edge. It is possible, therefore, that small bream avoid the L, making it a source of refuge from fish predation. Additionally, benthivorous feeding (by the larger bream at these sites) stir up sediments thereby decreasing water clarity (Breukelaar et al. 1994) and resulting in the very low SD values at these sites. Reclassification of the small bream as a benthic taxon transforms the ZF (BB) - *D. hyalina* agg. response model to a linear one. It is impossible to state with any certainty whether the mechanism for the unimodal relationship between *D. hyalina* agg. and ZF is due to the limitation of bream to the OW or the reduction of the fishes' reactive distance. What is clear is that the unimodal response was an indirect ecosystem-based feedback mechanism, rather than the result of a direct predator-prey relationship. Total *Daphnia* distribution reflected these same indirect feedback mechanisms, with a unimodal response to ZF as with *D. hyalina agg.* It seems unlikely that the positive relationship with TP was the result of a direct mechanism. The area where *Daphnia* were least likely to occur in the L was predicted to be low TP and intermediate ZF. These conditions are likely to result in high water clarity. Thus, actual predation pressure may be large and perhaps the best refuge would be available in any macrophyte beds away from the edge of the lake.

The model of *Ceriodaphnia* occurrence in the L provides an illustration of the combination of direct and indirect effects of the forces structuring zooplankton communities. *Ceriodaphnia* is preyed upon by fish and, in the absence of predation, may be competitively excluded by Daphnids (Gliwicz 1990). The best predictors of *Ceriodaphnia* presence in the L were *D. cucullata* abundance and SD. The increasing probability of occurrence of *Ceriodaphnia* with rising *D. cucullata* density at the low end of the SD gradient was the opposite of the relationship between *Daphnia* and *Ceriodaphnia* in the OW, where the former tended to exclude the latter. The co-existence of competing pelagic species of different size has been observed in conditions where the reactive distance of fish is reduced (Gliwicz 2001). At low SD sites, where *D. cucullata* and *Ceriodaphnia* not only co-existed but displayed an association, it is likely that food availability was high and predation pressure was less intense, due to a water clarity mediated reduction in the efficacy of fish predation rather than an actual decrease in ZF abundance. In this same model the predicted increase in the likelihood of occurrence of *Ceriodaphnia* as SD increased may be attributed to two factors. Firstly, rising SD resulted in an expanded

reactive distance of ZF, increasing predation pressure on the largest species i.e. *Daphnia* (Gardener 1981). Thus, *Ceriodaphnia* may have been released from the competitive pressures exerted by larger species resulting in an almost certain occurrence. Secondly, elevated SD correlated with increasing PVI and *Ceriodaphnia* exhibited associations with plant beds. Thus, whilst SD may best predict the presence of *Ceriodaphnia* the mechanisms actually determining the presence of *Ceriodaphnia* include competition with *Daphnia* spp., alteration to ZF reactive distance and probably food availability.

The small-bodied cladoceran *B. longirostris* displayed an unequivocal response to fish predation pressure in the OW. In the absence of fish it is easily out-competed by larger-bodied species. As food availability increases, however, they become more likely to persist with larger bodied species at a given level of ZF abundance (Demott & Kerfoot 1982). Optimal conditions for the occurrence of *B. longirostris* are characterised by high food levels (Chla) and high ZF density.

It is the differences in a species realised niche between sites which make the modelling of species' habitat preferences difficult. For example, the lack of a statistically significant model for *S. mucronata* and the slightly ambiguous model for *Ceriodaphnia* spp. may result from the fact that their distributions in environmental space are limited by different combinations of factors at different sites. For example, *Ceriodaphnia* tend to occur in August where *Daphnia* have been excluded by predation by young of the year fish (Stansfield et al. 1997). The presence of *Daphnia* in August is, however, dependent on more that just ZF with PVI, SD and Chla also influential in determining its occurrence. Thus, whilst fish clearly play an important role in determining the occurrence of *Ceriodaphnia*, the precise ZF abundance required to reduce the *Daphnia* spp. abundance to the point where *Ceriodaphnia* may co-exist varied both between sites and habitats.

2.5.3 Benthic species in the open water

All sampling techniques contain some form of bias and the methods employed here are likely to have sampled the plant and bottom-dwelling species less effectively than pelagic species (Bottrell et al. 1976). Nevertheless, the results presented here suggest that the sampling effort was equal between sites, the results comparable and the species-environment associations modelled from the data on the whole veracious.

PVI was clearly the dominant variable influencing the presence of some species, namely *Alona* spp., *C. sphaericus, E. lamellatus, G. testudinaria* and *Simocephalus* spp., with the differing responses perhaps alluding to their ecological preferences. For example, *P. aduncus* tended to occur at intermediate PVI and the combined *Pleuroxus* taxa had a high likelihood of occurrence at the highest PVI. Whilst PVI was generally the best predictor, ZF density also influenced the distribution of some epiphytic species. Furthermore, where plants were present *A. harpae* was likeliest to occur at high and *Pleuroxus* spp. at lower ZF density. The data for *Simocephalus* spp. suggest a strong negative relationship with ZF. The paucity of sites with both high fish and high plant abundance resulted in the model's reliance on one site in this area and thus the variance, or deviance, was large. Additionally, the absence of *Simocephalus* spp. from UPTO (perhaps for reasons other than ZF or PVI), a low ZF site with high plants, resulted in the relationship not being significant.

UPTO is an anomalous site with very high PVI yet no plant associated species were collected in the OW. The unimodal relationship of *Simocephalus* spp. to PVI in OW and WL was driven by its absence from Upton and thus the decline in probability of occurrence at high PVI may be spurious. The lack of plant associated taxa at Upton may have been due to their actual absence, e.g. *Simocephalus* was not recorded in previous, more intensive surveys (Stansfield et al. 1997) and was not recorded in the surface sediments. UPTO is an unusual site in that it is dominated by *Najas marina* L., a relatively late growing macrophyte species which does not tend to reach significant levels of abundance until July and peaks in August/September (Stansfield et al. 1997). This results in very low macrophyte cover for the early parts of the growing season. *Simocephalus* spp., a large bodied species which lives attached to plants (Fairchild 1981), may be excluded by some aspect, perhaps dense architecture, of *N. marina* itself. Alternatively it may require higher PVI earlier in the growing season to establish a population and, therefore, the very low PVI previous to July may preclude its presence at UPTO. In other cases, the species were likely to have been present as their remains were recorded in relatively high numbers in surficial sediments e.g. *C. sphaericus* and *Pleuroxus* spp. (Chapter 4). Their absence in August may be due to seasonal variation in abundance as intense invertebrate predation can result in a late summer minima of benthic chydorids (Goulden 1971).

2.5.4 Benthic species in the lake edge

CCA indicated the importance of water SD and ZF in structuring the L community. The patterns of species-environment association were, however, not as clear and the variance explained was less than that in the OW. Similarly, GLMs of individual species responses for the L zone data provided a less clear indication of species distribution than on the OW, with no statistically significant model for a number of species. In spite of the reduced importance of PVI relative to the OW, several species had significant positive relationships to PVI. The likelihood of occurrence of a number of taxa was best predicted by ZF and SD. *Alona* spp. tended to occur in the L when SD was high whereas PVI did not add significantly to the model. High SD in the lake margins may result in prolific epipelic and epiphytic algal growth, perhaps indicating the reliance of *Alona* spp. on these attached forms. The lack of coverage of sites in the high ZF and high SD resulted in the low reliability in that area of the model. The mechanism behind the decreased likelihood of occurrence of *Alona* spp. at low ZF and high SD is unclear.

In conclusion most of the poor swimming species responded to either macrophyte PVI (in the open water in particular) and to SD (L and WL data), reflecting substrate choice and perhaps a degree of epipelic/detrital feeding in the margins. Additionally, several species responded to ZF with some tending to occur at higher levels of ZF, suggesting some size selective predation by fish of plant associated species. Alternative factors, such as invertebrate predation, may also structure the benthic cladoceran communities.

2.6 Conclusion

Eutrophication tends to impact shallow lakes at all trophic levels (Jeppesen et al. 2000). Notwithstanding the large trophic gradient in the data set, nutrients did not appear to be of primary importance in determining zooplankton community structure and/or abundance. The influence of nutrients, however, may be larger than is apparent here. Whilst it seems unlikely that nutrients have a direct effect on the zooplankton community, they will have direct and indirect effects on the factors which do verifiably shape zooplankton composition, e.g. SD, phytoplankton composition and abundance, predatory invertebrate

abundance, plant abundance, macrophyte species architecture and fish community. For example, nutrient reduction has been shown to have a relatively rapid impact on various components of shallow lakes from plankton to fish (Jeppesen et al. 2005). Thus, a robust model of the relationship between zooplankton community composition, or individual species, and nutrients is not viable.

The greatest, and perhaps least addressable, assumption in all of the analysis presented here, and indeed in all static modelling, is that the communities are in equilibrium. In the dynamic environment of a lake in mid-summer this assumption is at best questionable. Despite the specious assumption of equilibrium, there were discernible patterns across 39 sites indicating that the communities, or a sufficient number of them, were near equilibrium or pseudo-equilibrium. A proportion of the 'noise' in the data almost certainly results from the failure to meet this assumption. Further sources of error in these models may derive from responses of fish and zooplankton to phenomena such as the behavioural cascade (Romare & Hansson 2003). This is a phenomenon where at the same or similar ZF density the presence of piscivores forced roach, a zooplanktivore, into taking refuge in plant beds which in turn forced *Daphnia* into the open water resulting in *Daphnia* spending more time in the OW than in the absence of the piscivore.

The data presented here unequivocally demonstrate that zooplanktivorous fish exert the strongest direct structuring force on the zooplankton community of shallow lakes. There are, however, a number of factors and mechanisms which complicate this relationship. Macrophyte abundance provides essential substrate for some species and refuge from predation for others. Water clarity not only best summarised the 'complex gradient' of variation in trophic structure and function in the data set, but also affected the predator-prey relationship through modification of the reactive distance of fish. The nature of the interactions between the variables shaping the zooplankton community were altered dependent upon the values of those very parameters, both absolutely and relative to one another. In addition, whilst not directly evident, in a statistically significant sense, from the data presented here it is likely that nutrient levels have some, albeit indirect, influence in shaping community structure (Jeppesen et al. 2000, Jeppesen et al. 2003b, Elser & Goldman 1991). Thus, the composition of the zooplankton community of shallow lakes is

dictated by a number of interacting factors, the strength and combination of these factors varies between species and for a single species may vary spatially within the same lake.

3 Chapter 3 - Is there a reliable animal-fossil relationship between contemporary and surface sediment cladoceran assemblages?

3.1 Introduction

Zooplankton is a key component of aquatic ecosystems, its community structure reflecting a combination of physical, chemical and biological characteristics of the system it occupies (Jeppesen et al. 2003a, 2003b). Analysis of the sedimentary remains of zooplankton including carapaces, post-abdomens, claws, mandibles, sections of antennae and ephippia in both surface sediments and older core material is well established (Frey 1960a, Whiteside 1970, Kerfoot 1974, Hann 1989, Leavitt et al. 1989, Korhola & Rautio 2000, Jeppesen et al. 2001b). Sub-fossil remains have been utilised in many studies investigating *inter alia*: past chydorid diversity (Whiteside & Harmsworth 1967); macrophyte coverage (Thoms et al. 1999); lake ontogeny (Frey 1958); trophic state (Boucherle & Züllig 1983, Stansfield et al. 1989, Hann et al. 1994, Hofmann 1996); lake-level changes (Sarmaja-Korjonen & Alhonen 1999); saline transgressions (Sarmaja-Korjonen & Hyvärinen 2002) and to track cycles in predation pressures (Kerfoot 1981). Sedimentary cladoceran assemblages have also been employed, alone and in combination with other palaeo-indicators, to track shifts in food web structure in response to liming (Kitchell & Kitchell 1980), an acidification episode (Sarmaja-Korjonen 2002) and fish removal and introduction (Leavitt at al. 1989, Leavitt et al. 1994).

The chitinous exoskeletal remains of cladocerans are generally abundant in lake sediments (Frey 1960b, Hann 1989). Fossil populations are, however, by their very nature fragmentary, providing an incomplete picture of the community which led to their formation (Frey 1958). Several elements of zooplankton communities, particularly copepods and rotifers, are very poorly represented by sub-fossils (Rautio et al. 2000) and therefore have not generally been included in palaeoecological studies. Furthermore, cladocerans exhibit differential preservation in sediments (Hann 1989, Korhola & Rautio

2000). Thicker bodied species, such as chydorids and *Bosmina* spp. are represented by a number of body parts (carapace, head-shield, post-abdomen and post abdominal claw). Sub-fossil assemblages of these well preserved taxa have been shown to reflect past communities relatively well, with fossil assemblages in surface and annually laminated sediments providing an accurate reflection of contemporaneous populations (Hann at al. 1994, Leavitt et al. 1994, Whiteside 1970, Amoros & Jacquet 1987). Lighter bodied species, with thinner chitinous exoskeletons, principally *Daphnia* spp., *Ceriodaphnia* spp. and *Simocephalus* spp. tend to be represented solely by claws as the softer body parts are poorly preserved (Frey 1986). Head-shields may preserve better in sediments from extreme environments, such as the Arctic (Rautio et al. 2000) or Tibetan plateau (Davidson & Mische unpublished data).

As a result of the assumed under-representation of *Daphnia* and *Ceriodaphnia* in the sediment record (Frey 1960b, 1986) there has been little focus, until relatively recently (Jeppesen et al. 1996, 2002, 2003a), on the potential of non-chitinous remains, i.e. ephippia to provide sedimentary representation for these species. However, Jeppesen et al. (2003a), found a good agreement between the relative contribution to the population of *Daphnia* spp. in the water column and their percentage abundance in surface sediments. The more littoral *Ceriodaphnia* spp., however, showed less good agreement between contemporary and ephippial relative abundance.

In keeping with the general research paradigm of recent decades, quantitative transfer functions based on the composition of sedimentary zooplankton remains and on *Daphnia* ephippia size, have been developed and applied to infer past zooplanktivorous fish predation pressure (Jeppesen et al. 1996, 2001a, 2002), total phosphorus (TP) (Brodersen et al. 1998) and mean summer air temperature (Duigan & Birks 2000). Confident interpretation of the sedimentary cladoceran record, and by extension any inference model based on those assemblages, relies upon the existence of a reliable animal-fossil relationship. Here, the relationship between contemporary (C) zooplankton populations and the surficial-sediment (S) assemblages of 39 shallow lakes is examined. Given the distinct time periods represented by the two types of sample, differential preservation of species and the necessary reliance on both chitinous and ephippial remains, it is unlikely that species occurrence in the contemporary samples will correspond exactly with that in the

surface sediments. This study, therefore, seeks to establish the degree of similarity with which those forces shaping the zooplankton community are expressed by the contemporary and sub-fossil assemblages.

3.2 Methods

The contemporary sampling regime was outlined in Chapter 2.

3.2.1 Palaeoecological methods

Surface sediment samples (0-1 cm) were collected in the U.K. using a Glew corer (Glew 1991) in November 1999 and in Denmark with a modified Hon-Kayak corer (Renberg 1991) in October 2003. In all cases the sample was extracted from approximately the centre of each lake. The top 0-1 cm of sediment of a shallow lake is typically the accretion of material deposited over a period of approximately 1-5 years, dependent upon lake productivity (Frey 1987, Anderson & Battarbee 1992). The method of enumeration used here is an adaptation of the sub-fossil cladocera preparation technique described by Korhola & Rautio (2001) and the method of Jeppesen et al. (1996). A sample of at least 5 cm^3 of sediment was analysed for ephippial remains using a binocular microscope at X 4-40 magnification. Ephippia enumerated in this way were expressed as numbers per 100 cm^3 of wet sediment. The sample was subsequently heated in a deflocculating agent (KOH) and sieved at 150 μm and 50 μm. The remains retained by the two sieves were then washed into separate pots and stained with safranin. Sub-samples were analysed using a compound microscope at X 40-400 magnification and the chitinous remains of the cladocera were identified with reference to Flössner (1972), Frey (1958, 1959) and Alonso (1996). Carapaces, head-shields and post-abdomens were recorded separately and the minimum possible number of individuals was calculated (Frey 1986). A total of at least 500 individuals per sample was counted from a sub-sample of known volume.

3.2.2 Data sets

The August values of TP, SRP, EC, pH, alkalinity, dissolved oxygen, Chlorophyll-*a* (Chla), nitrate, secchi depth and macrophyte percentage volume infestation(APVI), were used as

the environmental variables for the contemporary (C) data. As the surface sediment (S) assemblages represent a time period of at least a year, summer means of the environmental variable were used in this analysis. In most cases summer means were derived from monthly visits between April and September. The exceptions were APVI and fish density where the same measurements were used in both the C and S analyses were used in the analysis.

As described in Chapter 2 the live zooplankton populations were sampled in two ways, using a tube sampler in the open water and a net sweep at the lake edge. The data from the two methods of sampling the C environment were combined to create a whole-lake percentage relative abundance. The lake-edge and open-water abundances were converted to proportions then weighted by the area of the lake occupied by each habitat, determined by a GIS, and summed to create a whole-lake relative abundance for each species. The first few instars of copepods were excluded prior to converting the abundances to percentages as they numerically dominated some sites. The taxonomic resolution of the *Daphnia* guild was reduced; *D. galeata*, *D. cucullata* and *D. hyalina/longispina* were grouped into *D. hyalina* agg. in order to give a level of taxonomic resolution corresponding to that attainable with ephippia. Similarly *S. vetulus* and *S. expinosus* were amalgamated to *Simocephalus* spp. The *B. longirostris* varieties were reduced to species level.

3.2.3 Numerical methods and data manipulation

Given the stated aims of comparing whole-community response to the environmental gradients for the two data sets it was necessary to combine the chitin and ephippia based data to form a harmonised sedimentary data set. Chitinous remains are deposited in the sediment as they are shed as cladocera grow, thus each individual may potentially leave many remains. Ephippia are the product of sexual reproduction which occurs once or twice a year, dependent upon species and on environmental conditions. Thus, very few individuals result in ephippia (Korhola & Rautio 2000). This differential formation presented a number of problems in harmonising the two data types. The use of absolute numbers g^{-1} wet weight or dry weight underestimated the importance of the generally much rarer ephippia. Calculating chitinous and ephippial relative abundance separately and then combining the data (with a total of 200%) was also problematic as there were large differences in the total number of ephippia per sample. This resulted in the spurious

inflation of the importance of rare species at sites with a low abundance of ephippia. For example, a site with a total of 10 ephippia per 100 cm^3, all of which were *D. hyalina* agg., would have 100% for *D. hyalina* agg., whereas a site with a total of 300 ephippia per 100 cm^3, 150 of which were *D. hyalina* agg. ephippia would have a percentage relative abundance of just 50%. The solution reached here was to combine the relative abundance of chitinous remains with a relative abundance, weighted by the site's total ephippial abundance for those species represented best by ephippia, i.e. *D. magna*, *D. pulex*, *D. hyalina* agg., *Ceriodaphnia* spp. and *Simocephalus* spp. The relative abundance based on ephippial remains of each species was calculated and then weighted according to the total number of ephippia per 100 cm^3 in the sample. The weighting was based on the numerical distribution of total ephippia per 100 cm^3 across the 39 sites (Appendix 3).

Ordination is effective in investigating the patterns and causes of variation in multivariate data sets (ter Braak & Prentice 1988). Here, a combination of detrended correspondence analysis (DCA) (Hill 1973, Hill & Gauch 1980), constrained ordination both canonical correspondence analysis (CCA) and redundancy analysis (RDA) (ter Braak 1986, 1987, 1994) and partial constrained ordination (partial CCA & RDA) (Bocard et al. 1992) were employed. Ordination analysis was carried out using CANOCO version 4.5 (ter Braak & Smilauer 2002) on square-root transformed relative abundance data. Environmental data were either log, log (x+1) or square-root transformed depending on which transformation best approximated a normal distribution of the data. In DCA rare species were down-weighted and detrending was carried out in segments and non-linear rescaling was applied.

In order to further explore the similarities in the community-environment relationship between the C and S data sets, and to test the significance of any relationship found, Procrustes rotation and the PROTEST permutation test were applied to the ordination results (Jackson 1995, Peres-Neto & Jackson 2001). Procrustes rotation assesses the overall degree of correlation association between two or more ordination results by applying a Procrustean superimposition approach, where the results of the ordinations are scaled and rotated to find an optimal superimposition that maximizes their fit. The sum of the squared residuals between configurations in their optimal superimposition can be used as a metric of correlation (Gower 1971). PROTEST is a permutation-based procedure (Jackson 1995) which assesses the degree of concordance between two matrices, producing a correlation-

like statistic derived from the symmetric Procrustes sum of squares, referred to as m_{12}, and an associated P value indicating the likelihood of the relationship occurring by chance. The Procrustes analysis and PROTEST were carried out in R (The R Foundation 2004) using the vegan library.

3.3 Results

A total of 40 taxa were recorded in the C and 44 taxa in the S samples. The frequency of occurrence, median, mean and maximum values of relative abundance for the selected taxa (those occurring at > 2% of sites) (Table 3-1) demonstrated that despite their relatively high occurrence in the water column no recognisable remains of several pelagic species, namely Copepods, *Polyphemus pediculus* L., *S. mucronata* and *Diaphanosoma brachyurum* Liéven, were evident in the S assemblages. At the whole data-set scale, all other taxa recorded in August were represented palaeoecologically. It was relatively rare that a live sampled species was not found in the sediments at that site; when this did occur the relative abundance of that species in the water column was generally very low (Table 3-2). Consistent with previous work a single S sample provided a more complete species list for chydorids than the multiple samples from the contemporary environment (Frey 1960b).

Detrended correspondence analysis (DCA) of the community data indicated a larger variability in community composition between sites in the C compared to the S assemblage. This was reflected by a first axis length of 3.1 SD units in the C data as opposed to 1.8 SD for the S data. The reduction of the taxonomic resolution of the water column data, to the level where it corresponded to that obtainable in the S resulting in the DCA first axis length falling to 2.4 SD. A data set with a standard deviation, on its first axis of variation, of less than two is considered to have low variability within the data and linear methods (PCA and RDA) are deemed appropriate for data analysis (Gauch 1982, Birks 1995). Thus, linear methods were appropriate for the analysis of the surficial sediment assemblages. ter Braak & Prentice (1988) stated that where the first axis length falls between 1.5 and 3 SD units both linear (PCA/RDA) and unimodal (CA/DCA/CCA) methods "can be used to good effect". Thus, in order to provide the most rigorous comparison possible both data sets were

analysed using RDA, CCA, partial RDA and partial CCA. Given the lengths of the first axes in DCA, RDA was likely to be the most appropriate method for the S data and RDA or CCA for the C data.

Table 3-1. Comparison of the species information of the contemporary and surface sediment weighted relative abundances for selected species.

Species	Sedimentary occurrence	Water column occurrence	**Sites in common**
Acroperus harpae	34	10	**10**
Alona affinis	36	8	**8**
Alona costata	6	1	**1**
Alona guttata/rectangula	38	6	**6**
Alona guttata var. *tuberculata*	10		**0**
Alona guttata	22	5	**5**
Alonella nana	31	7	**7**
Alona quadrangularis	35		**0**
Alona rectangula	29	3	**2**
Alona rustica	5		**0**
Alonella exigua	3		**0**
Alonella excisa	5		**0**
Bosmina coregoni	2		**0**
Bosmina longirostris	37	28	**28**
Camptocercus rectirostris	22		**0**
Chydorus piger	4		**0**
Chydorus sphaericus	39	22	**22**
Diaphanosoma brachyurum		15	**0**
Disparalona rostrata	12		**0**
Eurycercus lamellatus	36	8	**8**
Graptoleberis testudinaria	28	4	**3**
Ilyocryptus sordidus	4		**0**
Leydigia acanthercoides	10		**0**
Leydigia leydigii	31	1	**1**
Leptodora kindti	1		**0**
Monospilus dispar	2		**0**
Pleuroxus aduncus	31	19	**16**
Pleuroxus denticulatus	14	3	**2**
Pleuroxus laevis	8	3	**3**
Pleuroxus trigonellus	1		**0**
Pleuroxus truncatus	12	9	**7**
Pleuroxus uncinatus	32	4	**4**
Polyphemus pediculus		5	**0**
Pseudochydorus globosus	3		**0**
Scapholeberis mucronata		23	**0**
Sida crystallina	5		**0**
Cyclops		39	**0**
Diaptomus		27	**0**
Ceriodaphnia spp.	35	31	**28**
Daphnia hyalina agg.	33	28	**24**
Daphnia magna	9	5	**4**
Daphnia pulex	10	7	**3**
Simocephalus spp.	14	15	**10**

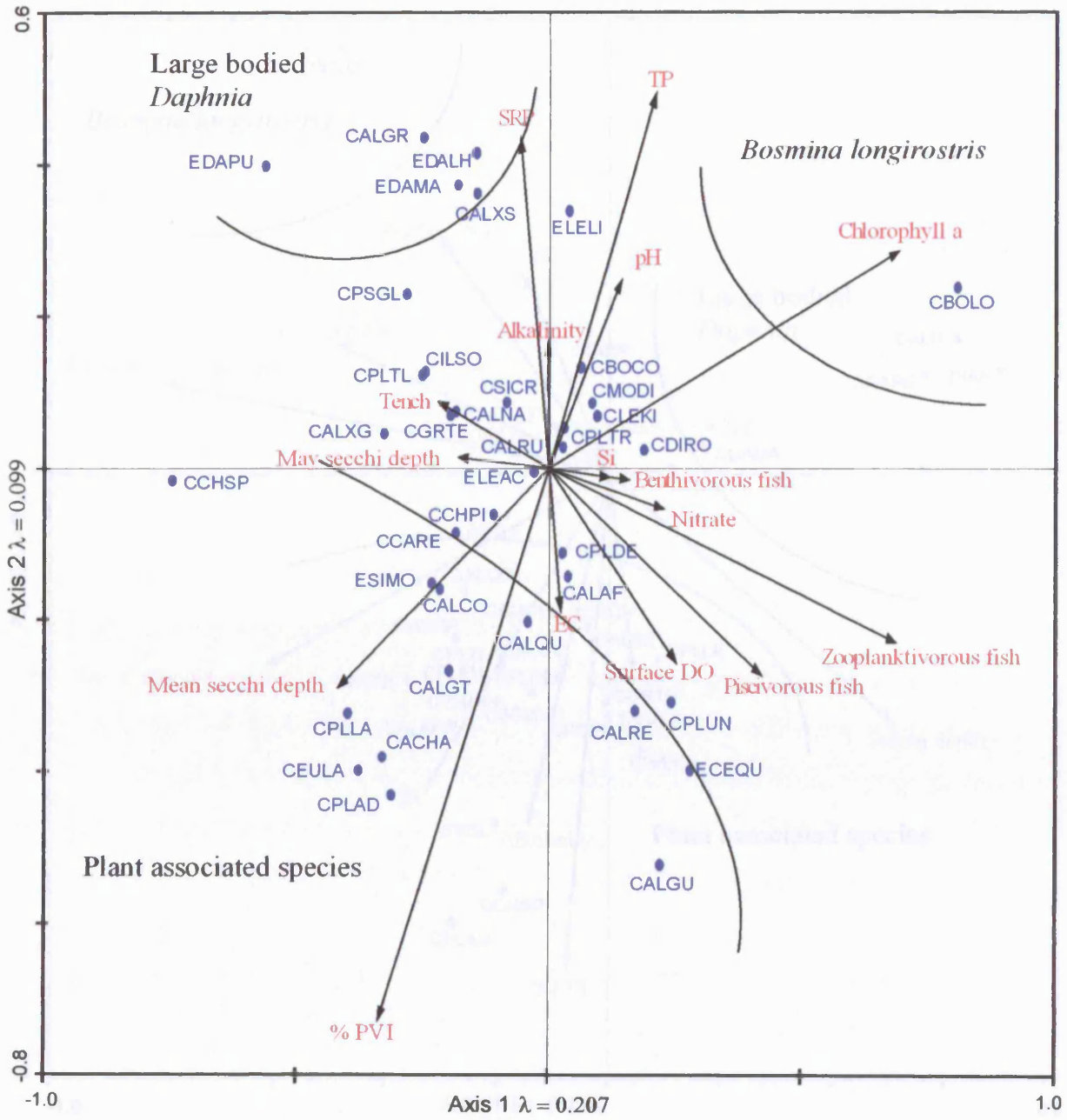
Table 3-2. Details of the relative abundance of species recorded in August samples which were absent from the surface sediment assemblage at that site.

Species	Occurrence in sedimentary data compared to contemporary data	% weighted relative abundance in August where absent in sediment sample
Alona rectangula	2 of 3	0.03
Graptoleberis testudinaria	3 of 4	0.005
Pleuroxus aduncus	16 of 19	0.05, 0.06, 0.34
Pleuroxus denticulatus	2 of 3	0.24
Pleuroxus truncatus	7 of 9	0.14, 0.5
Ceriodaphnia spp.	28 0f 31	3.08, 1.52, 1.06
Daphnia hyalina agg.	24 0f 28	0.62, 0.72, 0.16, 0.02
Daphnia magna	4 of 5	0.05
Daphnia pulex	3 of 7	0.36, 4.06, 1.01, 0.28
Simocephalus spp.	10 0f 15	0.23, 1, 8, 14 0.74

3.3.1 Comparing constrained ordinations

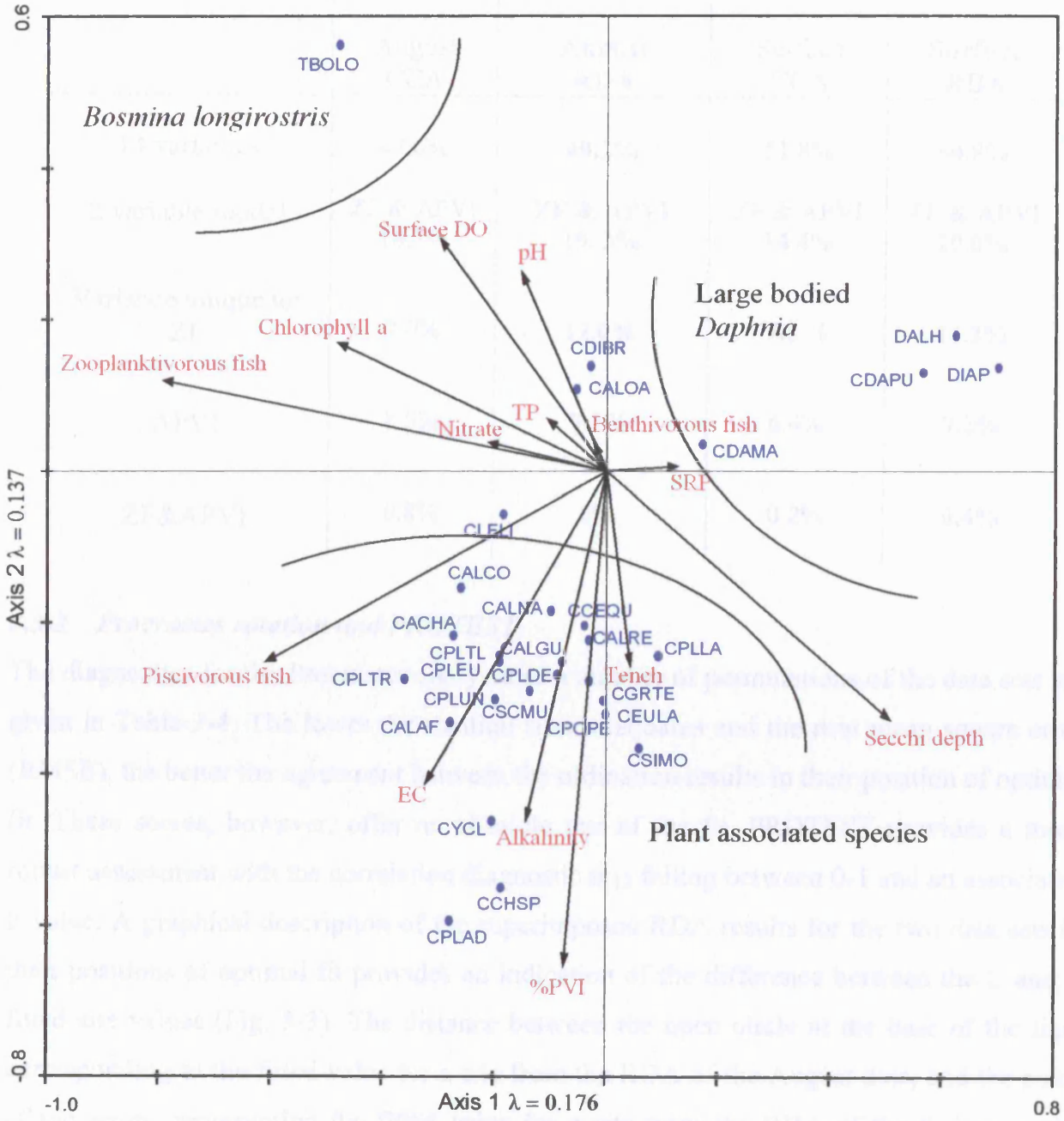
The constrained and partial constrained ordinations indicated that a very similar proportion of the variance within the C and S assemblage data was attributable to the suite of 14 environmental variables (Table 3-3). Notwithstanding slight differences in the location of most species there was in general a good level of agreement in the pattern of species distributions in ordination space between the data sets (Fig. 3-1 & 3-2). In particular, pelagic species e.g. large bodied *Daphnia* spp, the smaller *B. longirostris* and intermediate sized *Ceriodaphnia* spp. and plant associated Chydorids, displayed a similar magnitude of response to the same environmental variables in both data sets. Forward selection with Bonferonni correction (Legendre & Fortin 1989), indicated that chlorophyll-*a* (Chla) zooplanktivorous fish (ZF) and macrophytes abundance (PVI) were the most significant variables, explaining 25.1% of the variance in the S data. The significant explanatory variables for the C data were ZF and PVI, explaining 18.3% of the variance (Table 3-3).

Figure 3-1. RDA of sub-fossil cladoceran assemblage from 39 lake data set constrained by TP (µg l^{-1}), SRP (µg l^{-1}), EC (µS cm^{-3}), pH, alkalinity (mg l^{-1} $CaCO_3$) , dissolved oxygen (% saturation), Chlorophyll-*a* (µg l^{-1}), Nitrate (mg l^{-1}), both mean and May only SD (cm), August macrophyte PVI, ZF (no. m^{-2}), Piscivorous fish (no. m^{-2}), Benthivorous fish (no. m^{-2}), and Tench (no. m^{-2}).



Taxa are (a) CACHA – *Acroperus harpae*; CALAF – *Alona affinis*; CALGU – *Alona guttata*; CALNA – *Alonella nana*; CALRE – *Alona rectangula*; CBOLO – *Bosmina longirostris*; ECEQU – *Ceriodaphnia* spp.; CCHSP – *Chydorus sphaericus*; EDALH – *Daphnia longispina/hyalina*; EDAMA – *Daphnia magna*; EDAPU – *Daphnia pulex*; CEULA – *Eurycercus lamellatus*; CGRTE – *Graptoleberis testudinaria*; CLELI – *Leydigia leydigii*; ELEAC – *Leydigia acanthercoides*; CPLAD – *Pleuroxus aduncus*; CPLUN – *Pleuroxus uncinatus*; CPLDE – *Pleuroxus denticulatus*; CPLLA – *Pleuroxus laevis*; CPLST – *Pleuroxus striatus*; CPLTL – *Pleuroxus trigonellus*; CPLTR – *Pleuroxus truncatus*, CSICR - *Sida crystallina*; ESIMO – *Simocephalus* spp.

Figure 3-2. RDA of the weighted relative abundance of the August sampled zooplankton community constrained by August values of TP (µg l^{-1}), SRP (µg l^{-1}), EC (µS cm^{-3}), pH, alkalinity (mg l^{-1} $CaCO_3$), dissolved oxygen (% saturation), Chlorophyll-*a* (µg l^{-1}), Nitrate (mg l^{-1}), secchi depth (cm), August macrophyte PVI, ZF (no. m^{-2}), Piscivorous fish (no. m^{-2}), benthivorous fish (no. m^{-2}) and tench (no. m^{-2})



Taxa are (a) CACHA – *Acroperus harpae*; CALAF – *Alona affinis*; CALGU – *Alona guttata*; CALNA – *Alonella nana*; CALOA – *Alona* spp.; CBOLO – *Bosmina longirostris*; CBOLOC – *Bosmina longirostris var. cornuta*; CBOLOS – *Bosmina longirostris var. similis*; CCEQU – *Ceriodaphnia* spp.; CCHSP – *Chydorus sphaericus*; COPE – Copepodite; CYCL – Cyclops; CDACL – *Daphnia cucullata*; CDAGA – *Daphnia galeata*; DALH – *Daphnia longispina/hyalina*; CDAMA – *Daphnia magna*; CDAPU – *Daphnia pulex*; DIAP – *Diaptomus*; CDIBR – *Diaphanosoma brachyurum*; CEULA – *Eurycercus lamellatus*; CGRTE – *Graptoleberis testudinaria*; CLELI – *Leydigia leydigii*; CPLAD – *Pleuroxus aduncus*; CPLUN – *Pleuroxus uncinatus*; CPLDE – *Pleuroxus denticulatus*; CPLLA – *Pleuroxus laevis*; CPLST – *Pleuroxus striatus*; CPLTL – *Pleuroxus trigonellus*; CPLTR – *Pleuroxus truncatus*, CPOPE – *Polyphemus pediculus*; CSCMU – *Scapholeberis mucronata*; CSIEX – *Simocephalus expinosus*; CSIVE – *Simocephalus vetulus*.

Table 3-3. Summary results for partial CCA/RDA analysis on the contemporary and surface sediment data sets. Only the results of the 2 component models are given in order to facilitate comparison of the data sets. Variance unique to ZF (Zooplanktivorous fish), APVI (August PVI) and their co-variation terms are given.

	August CCA	**August RDA**	Surface CCA	**Surface RDA**
14 variables	47.6%	**49.2%**	51.8%	**54.8%**
2 variable model	ZF & APVI 18.3%	**ZF & APVI 19. 3%**	ZF & APVI 14.4%	**ZF & APVI 20.0%**
Variance unique to: ZF	9.0%	**12.0%**	7.8 %	**11.2%**
APVI	8.5%	**7.3%**	6.4%	**9.2%**
ZF&APVI	0.8%	**0%**	0.2%	**0.4%**

3.3.2 Procrustes rotation and PROTEST

The diagnostics for the Procrustes analyses of a number of permutations of the data sets are given in Table 3-4. The lower the rotation sum of squares and the root mean square error (RMSE), the better the agreement between the ordination results in their position of optimal fit. These scores, however, offer no absolute test of the fit. PROTEST provides a more robust assessment with the correlation diagnostic m_{12} falling between 0-1 and an associated P value. A graphical description of the superimposed RDA results for the two data sets in their positions of optimal fit provides an indication of the difference between the C and S fitted site values (Fig. 3-3). The distance between the open circle at the base of the line, corresponding to the fitted value for a site from the RDA of the August data, and the point of the arrow, representing the fitted value for a site from the RDA of the S data, is the Procrustes residual. This residual is an expression of the difference between the fitted ordination site scores of the C and S zooplankton community composition. Procrustes and PROTEST analyses indicated a highly significant concordance between the data sets (Table 3-4) with the correlation score (m_{12}) increasing if RDA was replaced with CCA for the lake water samples, and increasing still further if copepod data were excluded. Copepods were not represented in the S data (Table 3-4).

Table 3-4. Procrustes Rotation and PROTEST diagnostics for comparison of surface sediment RDA and three permutations of the WL analysis, RDA, CCA and CCA with copepod data removed.

Test	Procrustes rotation sum of squares	Procrustes RMSE	PROTEST m_{12}	P value
Surface sediment RDA and WL RDA	88.84	1.509	0.5152	< 0.001
Surface RDA and WL CCA	82.65	1.456	0.5627	< 0.001
Surface RDA and WL CCA with copepod data removed	72.44	1.363	0.6333	< 0.001

Several sites had very low Procrustes residuals indicating a high level of agreement in their ordination positions between the data sets (e.g. Lily Broad (LYLI), Beeston Hall Lake (BEES), Blickling Hall Lake (BLIC), Bonderup (BOND), Buckenham Broad (BUCK), Cromes Broad (CROM) and Salhouse Little Broad (SALH)). There were, however, a number of sites which displayed a low degree of similarity in their ordination results (Fig. 3-3). The direction of movement between the base and the end of the arrow is related to the environmental variables with which the ordinations are constrained (Fig. 3-3). The movement between the base and the arrow point for Scottow Pond (SCOT) is illustrative of this. The C community was dominated by copepods with very low *Daphnia* abundance, whereas the S assemblage contained relatively large numbers of *Daphnia* ephippia and *P. laevis* exoskeletal remains (Appendices 2 & 4). *Daphnia* were negatively associated with high ZF density and *P. laevis* was strongly associated with high PVI (Fig. 3-1 & 3-2). Therefore, not only is the distance moved in the plot (Fig. 3-3) an indication of the disparity between C and S data but the direction of the movement is a reflection of the environmental associations of the species that make up the assemblage of a particular sample. Therefore, the point of the arrow, corresponding to the S assemblage, for SCOT reflects lower ZF density but no reduction in PVI compared with the C data shown by the base of the arrow.

Those sites with the highest Procrustes residuals (>2) tended to have very low ZF density (Fig. 3-4) and could be divided into two types. The first (Green Plantation Pond (GREP), UPTO and Narford Hall Lake (NARF)), were characterised by a dramatic movement towards high PVI between the C and S samples. In the second group, (Gammelmose

(GAMM), Saham Toney Mere (SAHA) and Sorte Sø (SORT)) there was a shift away from high PVI and towards a low ZF density between the C and S assemblages.

Figure 3-3. Procrustean superimposition plot, a plot of the superimposed data matrices in their position of optimal fit, generated from the ordinal results of the RDAs. The circle at the base of the line represents C data set (August samples) and the point of the arrow the S data set (surface sediments). The distance is the Procrustean residual, representing the difference between the two. Inset is the graphical representation of the environmental variables.

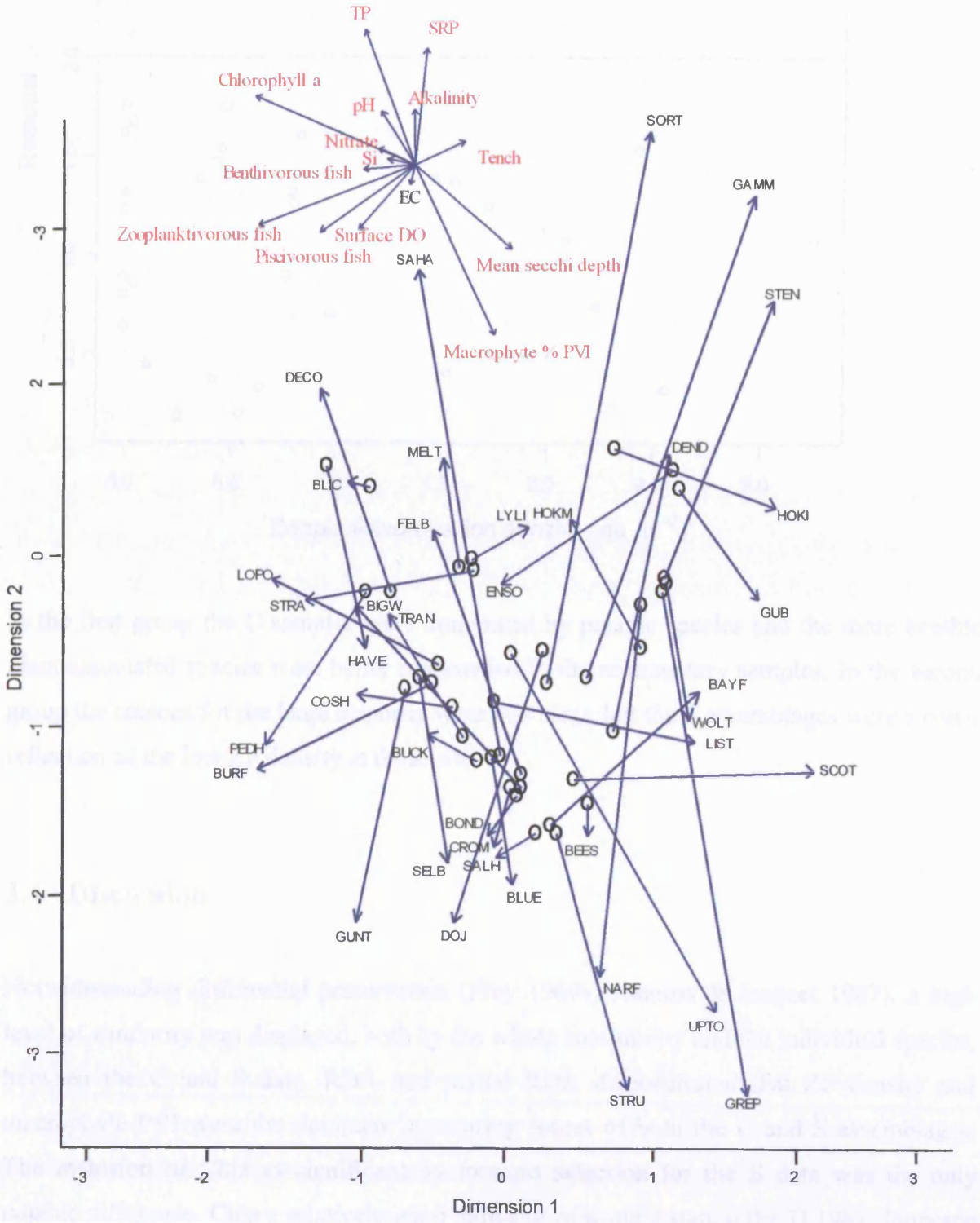
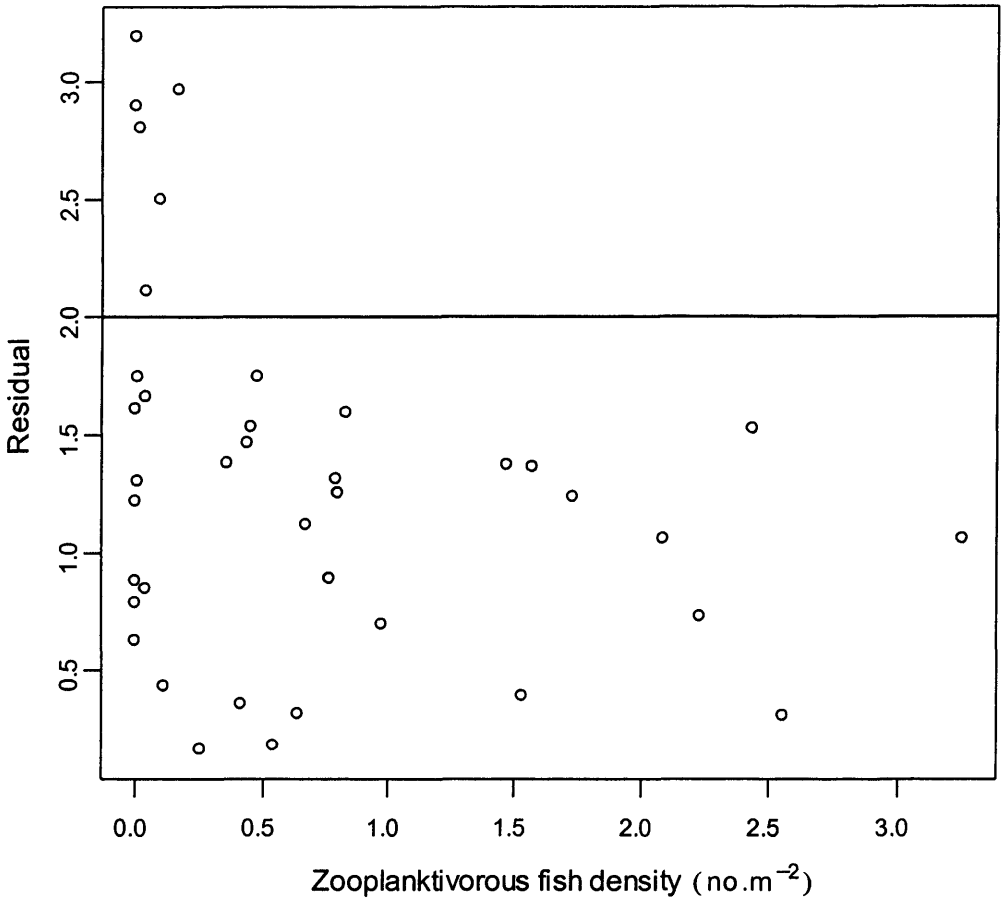


Figure 3-4. Plot of zooplanktivorous fish density against residuals from Procrustean analysis.



In the first group the C samples were dominated by pelagic species and the more benthic plant-associated species were better represented in the sedimentary samples. In the second group the reasons for the large disparity were less clear, but the S assemblages were a better reflection of the low ZF density at those sites.

3.4 Discussion

Notwithstanding differential preservation (Frey 1960a, Amoros & Jacquet 1987), a high level of similarity was displayed, both by the whole community and the individual species, between the C and S data. RDA and partial RDA demonstrated that ZF density and macrophyte PVI were the dominant structuring forces of both the C and S assemblages. The inclusion of Chla as significant by forward selection for the S data was the only notable difference. Chla a relatively good indicator of trophic state (OECD 1982, Jeppesen

et al. 2000) and it had a very high variance inflation factor (VIF) >4 in the surface sediment RDA, indicating high degree of co-linearity with other variables. In contrast, ZF and PVI both had low VIFs <2. The large co-variation terms between PVI-Chla and ZF-Chla, confirmed the linked nature of change along the trophic gradient (Jeppesen et al. 2000). The latter, in particular, indicates the cascading effect of fish on phytoplankton crop via the cladoceran community (Carpenter et al. 1985).

Cladoceran communities, both pelagic and plant-associated species, vary seasonally (Goulden 1971, Stansfield et al. 1997). Macrophyte PVI and predation pressure from ZF increase to near maximum in August (Jeppesen et al. 2003b, Whiteside 1988). The C data, therefore, were sampled at a period of intense fish predation and very high PVI. The surface sediment samples, on the other hand represent an accretion of between approximately 1 and 5 years of deposition. Fish predation pressure and PVI both decline outside the seasonal peaks of mid to late summer. It has been demonstrated, however, that ZF continue to structure the cladoceran communities outside the main growing season (Jeppesen et al. 2004). Chla directly effects cladocerans in terms of food quantity (Vanni 1987), and is additionally a relatively good general indicator of trophic state. It is therefore, unsurprising that it was selected as a variable important in shaping the sedimentary cladoceran assemblage. When the highly co-linear Chla was excluded from the variance partitioning procedure the proportion of variance explained by ZF and submerged plant abundance was almost identical in both S and C data. This indicates that the primary importance of predation pressure and macrophyte abundance in structuring the zooplankton communities of shallow lakes is reflected equally by both the C and the S data.

No one method effectively samples the entire cladoceran community (Bottrell et al. 1976). Sampling techniques used in the contemporary environment tend to have a bias toward pelagic species. In this study an attempt to allow for this was made by sampling in plant beds, where they were present, on a visual transect from the centre towards the lake edge and through sampling the edge communities with a series of net sweeps. Nonetheless, the effects of the bias towards pelagic species were still apparent in those sites with high PVI, such as SCOT and others with high water clarity and low PVI e.g. NARF. The high numbers of epiphytic and benthic species in the S samples, not recorded in the C data, resulted in large Procrustes residuals. The disparity between the data matrices was

exacerbated when the copepods, unrecorded in the S data, dominated in the C. This is illustrated by the larger m_{12} statistic when copepods were excluded from the PROTEST analysis.

Those sites with very high Procrustes residuals fell into two very distinct groups: UPTO, NARF and GREP had relatively low Chla, low TP and relatively high PVI; whereas GAMM, SAHA and SORT had very few or no submerged plants, very high TP and higher Chla. The ecological functioning of the two groups was likely to be very different with each group representing opposite ends of a spectrum. One end was dominated by benthic/macrophyte forms of production and the other by pelagic productivity (Vadeboncoeur et al. 2003). In the latter group, where significant numbers of benthic species were present they were probably utilising detrital resources rather than exploiting benthic algal production, e.g. the high proportion of *Alona guttata/rectangula* in the surface sediments of the extremely turbid SORT. These sites, which all had very low ZF density, may indicate that at the extremes of the ecological functioning gradient there are more likely to be large differences between the C and S assemblages. Nonetheless in general the data suggest that sub-fossil and C assemblages reflect the same structuring forces to very similar degrees.

In keeping with the findings of Jeppesen et al. (2003a) the analyses presented here suggest that the ephippial remains of important pelagic species (*Daphnia & Ceriodaphnia*) are a relatively good reflection of their presence in the contemporary environment. Additionally, a weighted relative abundance of total ephippia provided a means by which chitinous and ephippia data could be harmonised, allowing multivariate analysis of a more complete data set and direct comparison with the extant community.

Shallow lakes display a fairly well defined tendency of temporal succession from large populations of *Daphnia* to smaller pelagic species throughout the growing season attributed to both predation and food limitation (Lampert et al. 1986, Stansfield et al. 1997, Lueke et al. 1990, Hülsmann 2003). The profusion of large bodied herbivores in spring may lead to a clear-water phase (Lampert et al. 1986). In enriched lakes the dense populations of large *Daphnia* responsible for this period of clear water are generally absent by August, in particular where there is a lack of refuge from predation (Timms & Moss 1984, Wright &

Shapiro 1990). Thus, large amounts of *Daphnia* may occur in spring and leave their ephippia in the sediments where they were not sampled in August. Furthermore, the inter-annual stability of ecosystem functioning may also lead to differences between the C and the S data sets. Lakes with low TP, relatively high PVI, and relatively high percentage of piscivorous fish are likely to have stable ecosystem structure and function and zooplanktivory will be relatively constant. In contrast lakes with higher TP, high Chla, low piscivory and high zooplanktivory may well have less stability in ecosystem function both within and between years. For example, inter-annual variation in *Daphnia* occurrence and abundance can occur in phytoplankton-dominated sites due to a feedback mechanism with ZF recruitment. (Cryer et al. 1986). This may result in an inter-annual cycle between high abundance of *Daphnia,* relatively clear water conditions and low zooplanktivory and the obverse of turbid water, the absence of *Daphnia* by mid-summer and high ZF predation. This inter-annual variability in ZF may result in the surface sediments, laid down over one to five years, having been formed as a result of fish populations distinct from those sampled in the year that the surficial sediments were extracted. Thus, both seasonal and inter-annual variation in shallow lake ecosystem structure may have introduced some error may be introduced into the comparison of the C and S data sets.

In spite of the numerous sources of error entailed in the comparison of the modern and sub-fossil data, this study strongly indicates the existence of a reliable and predictable relationship between the two assemblages. Furthermore, the relative influence of the forces shaping the communities exhibited a highly significant concordance between the two data sets. Thus, the potential of cladoceran surficial sediment assemblages for modelling and ultimately tracking environmental change does not appear to be limited by a lack of parity between the contemporary and the sub-fossil data. The composition of the sedimentary community, based on a single central lake sample, responds in a coherent manner to changes in trophic structure and function across the training set. Therefore, cladoceran remains offer a great potential for tracking shifts in ecosystem structure and function.

3.5 Conclusions

Sedimentary cladoceran remains have long been used to track changes in aquatic systems. The reliability of the live animal–fossil relationship at the whole community level has not previously been tested. Prior to this study, the absence of abundant representative remains of a number of important pelagic species, in particular *Daphnia*, has limited comparison to those species leaving abundant chitinous remains. Here, we have shown that chitinous and ephippial data can be combined thereby allowing the analyses of more complete community data and permitting a direct comparison with live sampled communities. This study found that there was a high level of similarity in the community response to the varying environment of the training set between the C community sampled in late summer and the assemblage analysed from a single S sample extracted from a central lake location. Therefore, analysis of cladoceran sub-fossil assemblages may provide a means with which to assess the degree of change in those forces that play a part in structuring the community (ZF density and submerged macrophyte PVI). Further, through the application of the analysis to core material it may be possible to assess the degree of temporal change in the ecological structure and function of shallow lake ecosystems.

4 Chapter 4 – The simultaneous reconstruction of past fish and macrophyte abundance in shallow lakes from sub-fossil cladoceran assemblages: A new approach to inferring past biology.

4.1 Introduction

Animal and plant remains in lake sediments reflect aspects of the physical, chemical and biological characteristics of the aquatic system from which they originate (Frey 1960a, Anderson & Battarbee 1994, Juggins 1992, Smol 1992, Jeppesen et al. 2001b). Sedimentary remains may, therefore, provide information on the environmental factors shaping the biological communities both in space and time. Sub-fossil assemblages have been employed both as descriptors of temporal variation in contemporary community structure, and to reflect broader environmental change. A number of different indicators have been utilised, including diatoms (Battarbee 1978, Haworth 1980), algal pigments (Vallentyne 1956, Leavitt 1993), cladocerans (Frey 1958, Hann 1989) and the macro-remains of aquatic plants (Fredskild 1983).

Recent decades have seen the development of inference models, or transfer functions, which have sought to quantify species response to an environmental variable. Transfer functions are developed by calibrating surface sediment assemblage data against contemporary measurements from a 'training set' of sites (typically >30) representing a gradient of the environmental variable of interest. Fossil assemblages from sediment cores then become a proxy, via some form of weighted averaging of the derived optima, for the past values of the inferred parameter. A number of different proxies have been employed to reconstruct a variety of past environmental conditions, *inter alia*: diatoms and lake-water pH (Flower & Battarbee 1984, Jones et al. 1989, Birks et al. 1990), salinity (Fritz et al. 1991), chlorophyll-*a* (Jones & Juggins 1995) and epilimnetic total phosphorus (TP) (Bennion et al. 1996, Hall & Smol 1999); chironomids and July air temperature (Brooks & Birks 2000) and hypolimnetic anoxia (Quinlan et al. 1998). In addition to inferring past

physical and chemical conditions, the same numerical techniques have been applied to reconstruct aspects of past biological structure, specifically planktivorous fish density and macrophyte abundance from cladoceran assemblages (Jeppesen et al. 1996, 1998, 2001a).

Notwithstanding impressive performance diagnostics with high r^2 and low root mean square error of prediction (RMSEP) a number of transfer functions may be unreliable when applied to core material (Bennion et al. 2001, Sayer 2001, Birks 2003). Whilst reconstructions generally infer temporal trends correctly, though there are cases where even the directional trend may be incorrect (Sayer 2001), the absolute values predicted by these models may be questionable (Fritz et al. 1993, Jeppesen et al. 2001b, Brodersen et al. 2004, Battarbee et al. 2005, Velle et al. 2005). In their review of cladoceran functional palaeolimnology Jeppesen et al. (2001b) noted that, in general, transfer functions based on ranges of environmental variance naturally exhibited by individual lakes (such as TP, organic C and zooplanktivorous fish (ZF)) were less accurate than those covering long environmental gradients (e.g. pH & salinity). For a model to have a generality of application outside the 'training set' from which it was constructed, it is desirable that the quantified species-environment relationship is based on a direct causal mechanism (Guisan & Zimmerman 2001). This frailty in application of some transfer functions may derive from either the absence of a direct causal relationship or where a direct relationship exists, there may be some structured error in the model prediction as a result of interactions with other, perhaps independent variables. Not only is it rare that one factor in isolation determines the presence, absence and abundance of a particular species, but the strength of the relationship may change and even disappear as other factors vary. For example, the importance of ZF density in structuring the zooplankton community may change with trophic status (Elser & Goldman 1991, Jeppesen et al. 2003b).

The complexity of the species-environment relationship in shallow lakes demonstrates why modelling species optima for one variable may contain significant errors. Pelagic cladocerans are vulnerable to predation by ZF, which selectively feed on larger zooplankton species and the larger individuals of a particular species (Brooks & Dodson 1965, Gardner 1981). Thus, it may be possible to quantify a shift in pelagic species composition in response to increasing fish predation. There are, however, a number of factors which interact with, and complicate, this predator-prey relationship. These include

macrophyte density (Timms & Moss 1984, Lauridsen & Lodge 1996), water clarity (Gardner 1981, Gliwicz 2001), phytoplankton abundance (Vanni 1987), pelagic and benthic invertebrate predation (Goulden 1971, Scheffer 1998) and benthivorous fish abundance (Breukelaar et al. 1994, chapter 2). The multiplicity of interactions between environmental variables determining the presence, absence and abundance of a species makes the reliable quantification of the response of a species to a single environmental variable unlikely. For example, two sites with the same ZF abundance but different water clarity and macrophyte abundances may result in very different levels of actual predation pressure and thus distinct zooplankton communities. Thus, a key assumption of the transfer function approach namely, that environmental variables, other than the one of interest, have no significant affect on community composition (Birks et al. 1990, Juggins 1992) is unlikely to be fulfilled. Indeed, the reported fallibility of the planktivorous fish catch per unit effort (CPUE) transfer function, developed by Jeppesen et al. (1996), in the presence of macrophytes is almost certainly due to a failure to meet this assumption.

In spite of the complexity of response, cladoceran sedimentary remains have been shown to be sensitive to changes in physical, chemical and biological variables, such as acidification, nutrient concentrations, lake-level changes and alterations in ZF density (Brooks & Dodson 1964, Boucherle & Züllig 1983, Lauridsen et al. 1986, Leavitt et al. 1989, Hann et al. 1994, Sarmaja-Korjonen & Alhonen 1999, Jeppesen et al. 2001a). The fact that cladoceran assemblages respond to so many different forces is an indication of their sensitivity to environmental change. This is attributable to their central position in the food-web and to a species being generally pelagic or benthic in habitat preference. As such, any change in ecosystem structure and function, such as a shift in the balance of benthic-pelagic productivity or a change in vertebrate or invertebrate predation pressure is likely to be reflected by change in some aspect of the cladoceran community. Cladoceran based transfer functions have utilised the differential sensitivity of the benthic and pelagic species to the changing environment. For example, Jeppesen et al. (1996) used almost exclusively pelagic species to reconstruct past planktivorous fish CPUE, whereas, Brodersen et al. (1998) employed solely chydorid cladocerans, which are generally benthic, to infer TP.

In shallow lakes the boundary between the benthic and the pelagic is more likely to be blurred than in deep lakes. Whilst species do have a general preference for either the

benthic or pelagic zones they may display a certain plasticity of behaviour. For example, research using the stable isotopes of carbon and nitrogen has shown that generally pelagic *Daphnia* spp. may also feed extensively on epiphyton (Jones & Waldron 2003). Conversely, the apparently plant associated *C. sphaericus* (e.g. Chapter 2) will become pelagic where superior competitors have been excluded by some factor, e.g. blue-green algae (Ghoudani et al. 2003). The use of plant-associated cladocerans to model macrophyte density may illuminate some of the problems associated with attempting quantitative reconstruction. A number of species of cladocerans, particularly chydorids, are plant associated (Fryer 1968) and the percentage abundance of their sedimentary remains reflects macrophyte density (Thoms et al. 1999). However, the plasticity of behaviour of some species (e.g. *C. sphaericus*), in combination with size selective predation of fish on larger species of plant associated cladocerans (such as *Sida* spp. and *Simocephalus* spp. (Blumenshine et al. 2000), has made the development of a cladoceran based macrophyte abundance transfer function problematic (Jeppesen et al. 2001b). Furthermore, the inherent noise in biological data, resulting from phenomena such as behavioural responses (e.g. Romare & Hansson 2003), competitive interactions and ecosystem feedbacks (Chapter 2) have thus far precluded the development of a model capable of reliable predictions of precise values of macrophyte abundance.

It is clear that cladoceran assemblages are sensitive to environmental change and therefore have potential for modelling a number of aspects of shallow lake ecology. However, the multiple structuring forces and the close benthic-pelagic coupling means established techniques modelling one explanatory variable in isolation are inappropriate. This study, therefore, seeks to develop an inference model, utilising the response of the entire cladoceran community, capable of simultaneously reconstructing multiple factors, in this case ZF and macrophyte abundance. Given the multiplicity and complexity of interactions in shallow lakes and the inherent noise in biological data, the assemblage-environment relationship does not lend itself to confident modelling of precise values of either variable. Thus, the specious pursuit of precision was eschewed in favour of developing a robust technique capable of reconstructing aspects of both ZF and submerged macrophyte abundance, and identifying shifts in the sub-fossil cladoceran assemblage coincident with significant changes in ecological structure and function.

4.2 Study sites

The study sites are described in Chapter 1.

4.3 Methods

Field and laboratory methods are outlined in Chapters 2 and 3.

4.3.1 Data manipulation and numerical methods

The cladoceran surface-sediment assemblage data presented here are outlined in Chapter 3. They combine relative abundance of chitinous remains with the weighted relative abundance of the ephippial data. For the multivariate regression tree analysis employed here those species present at less than 2% of the sites and where abundance was less than 1% at a site, were excluded from the analyses.

4.3.2 Ordination

A number of numerical techniques were employed to analyse the data set. Ordination, specifically Detrended correspondence analysis (DCA), redundancy analysis (RDA) and partial RDA, provided some initial insights into the structure of the data set and an indication of the relative importance of the various environmental variables in shaping the surface-sediment, sub-fossil assemblage. RDA is a robust technique for determining and explaining patterns in species data and provides an excellent way of visualising the data (ter Braak 1994, ter Braak & Prentice 1988). RDA biplots position each species according to the weighted average of its relative abundance, constrained by a linear combination of the environmental variables. Axis 1 is a linear combination of the environmental variables associated with the largest amount of variation in the biological assemblages. The vectors representing the environmental variables are positioned according to both their degree of correlation with each other and with the linear combination which explains the greatest amount of variance in the species data (i.e. the ordination vectors or axes). The length of the arrow reflects the relative importance of that variable in explaining the distribution of the species data (ter Braak 1994).

Ordination analysis was carried out using CANOCO version 4.5 (ter Braak & Šmilauer 2002) on square-root transformed relative abundance data. Environmental data were either log, log (x+1) or square-root transformed depending on which transformation best approximated a normal distribution of the data. Fourteen variables were used to analyse the surface sediment data were: TP, SRP, nitrate, EC, pH, May secchi depth (SD), mean SD, mean macrophyte percent volume infestation (MPVI), August macrophyte PVI (APVI), ZF density, piscivorous fish (PF) density, benthivorous fish (BF) density and tench density. In DCA rare species were down-weighted and detrending by segments was used.

4.3.3 Regression trees

Classification and regression trees (CART) employ binary recursive partitioning in order to model the species environment relationship and may be applied to univariate or multivariate data sets (De'ath 2002). Models of species response relative to a continuous predictor are termed regression trees (Breiman et al. 1984). This technique, sometimes termed constrained clustering, represents a marriage of cluster analysis and regression. The method successively splits species data, univariate or multivariate, along axes of predictor variables. Euclidean distance is used to summarise between-site differences in community composition. The stipulated explanatory variables are applied in turn and the parameter explaining most variation is selected. The sites are then split at the point on the axis of the explanatory variable that minimises the sum of squared distance (SSD) within the resultant groups and thus maximises the between-group SSD. The process is then repeated on the resultant groups, allowing alternative predictor variables to be selected at different levels of the resulting multivariate regression tree (MRT). The final groups of the MRT are termed 'leaves'. The amount of variance attributable to the predictor variables in the MRT model is determined by calculating the proportion of the SSD from the entire data set remaining in all the MRT 'leaves'. MRT analysis was an appropriate tool for modelling the data presented here, being capable of handling complex ecological data with mixed linear and non-linear responses to the underlying change and high-order interactions (Breiman et al. 1984, De'ath & Fabricus 2000, De'ath 2002).

Regression trees tend to provide an elaborate over-fitted model and therefore require simplification, generally based on some '*cost-complexity measure*' (Crawley 2002), which balances the fit of the model and its predictive power. In this study a cross validation test

was applied, by splitting the data, constructing a new model from a subset of samples and then testing the predictive accuracy of that model on those sample(s) not included in its construction. This process was repeated until each sample had been left out in turn and the cross-validated error stabilised. Thus, a more "honest" assessment of the model performance was attained (Breiman et al. 1984). De'ath and Fabricus (2000) state that it is appropriate to select either the model with the minimum cross-validated error, or the most complex tree within one standard error of the best predictive tree (Breiman et al. 1984). All MRT analysis was carried out in R 2.0.0 (R. Development core team 2004) using the mvpart library (De'ath 2002).

4.3.4 Characteristics of MRT defined groups

4.3.4.1 Mean abundance

The average abundance of the species most illustrative of the between-group differences are presented by bar-plots with 95% confidence limits calculated as follows:

$CL_{95\%} = t(0.05, df)\ \sqrt{S^2/n}$

where df = degrees of freedom, S^2 = variance and n = number of samples.

4.3.4.2 Indicator species

In order to determine which species characterised the final MRT designated groups and which were significantly associated with the splits in the tree, indicator species analysis (INDVAL) was employed (Dufrene & Legendre 1997). This is an index based on species relative abundance and frequency of abundance within the stipulated groups. The index takes values from zero to one hundred, the latter being where a species occurs at all the sites within a group but at no other site. The statistical significance of the species' association with a group or partition in the tree was determined by a random reallocation permutation test, with 500 iterations.

4.3.4.3 Box-plots

The ZF density, APVI, MPVI, TP, nitrate, Chla, mean SD and August SD for each MRT group were summarised by box plots.

4.3.4.4 Validation of MRT groups

In order to further establish the veracity of the selected model, analysis of similarity (ANOSIM) was carried out on the MRT designated groups. ANOSIM is a non-parametric permutation based procedure for assessing the significance of between-group differences (Clarke 1993). The ANOSIM R statistic varies between 0, representing an entirely random distribution of objects between groups, and 1, indicating perfect dissimilarity between all groups, and has an associated P value. ANOSIM analyses were again carried out in R 2.0.0 (R. Development core team 2004) using the vegan library.

The residuals of the MRT model were explored using RDA of the surface sediment assemblages with ZF and APVI as the constraining variables, with the sites entered into the analysis passively. The difference between the position of the active (constrained or fitted value) and passive sample in the biplot represents the model residual for that site. In addition this analysis represented a test of the MRT model veracity. The number of samples that change their MRT defined group between their active and passive sample also provided a measure of the accuracy of prediction.

4.4 Results

The 39 lakes in the 'training set' covered a long trophic gradient with a wide range of TP, SRP, Chla, nitrate and SD values (Table 4-1). There were a number of statistically significant correlations between the environmental variables in the data set (Table 4-2). In particular, there were significant positive correlations between TP and Chla and between mean PVI, August PVI and SD. The sites displayed large variations in aquatic MPVI, APVI, ZF, piscivorous fish density and sedimentary representation of several key cladoceran species (Table 4-3).

Table 4-1. Summary of summer mean, median, minimum and maximum values for the key chemical parameters for the 39 sites: Surface Area (SA-ha), Max depth (cm), Mean depth (cm), Chla ($\mu g\ l^{-1}$), TP ($\mu g\ l^{-1}$), SRP ($\mu g\ l^{-1}$), nitrate (NO^{-}_3-N-mg l^{-1}), EC (μScm^{-3}), pH, Alkalinity (Alk-mg $l^{-1}CaCO_3$), surface dissolved oxygen (DO-%sat), mean SD (cm).

	SA	Max depth	Mean depth	Chla	TP	SRP	NO^{-}_3-N	EC	pH	Alk	DO	SD mean
Min.	0.4	75	54	2	19.4	3	0	266	7.5	71	34	47.8
Median				19.2	88.8	20	0.12	524	8.1	162	108	127.8
Mean	4.6	166	103	27.8	227.9	135	0.52	552	8.2	167	105	130.2
Max.	22.5	450	212	85	4056	3065	2.66	1378	9	310	172	292

4.4.1 Ordination

A total of 44 cladoceran taxa were recorded in the surficial sediments (Appendix 4). There was a relatively low degree of species turnover in the data set as revealed by a short DCA axis one length of 1.8 SD. Thus, linear based RDA was an appropriate analytical tool (Legendre & Legendre 1998) with which to explore the species-environment relationships in the data. The RDA biplot provided some insights into species-environment relationships (Fig. 4-1). For example, *B. longirostris* correlated positively whereas *D. hyalina* agg. had a negative association with ZF. Several species of chydorid, in particular, *A. harpae, E. lamellatus* and *P. laevis* were strongly associated with APVI. *Ceriodaphnia*, an intermediate sized pelagic species, lay between the small bodied *B. longirostris* and the large bodied *Daphnia* species along the ZF gradient. This may indicate competitive exclusion by *Daphnia* at low ZF density and predatory exclusion at high ZF.

Forward selection with Bonferroni correction (Legendre & Fortin 1989) indicated that ZF and APVI and Chla provided the most parsimonious explanation of the variation in the sedimentary cladoceran assemblage (Fig. 4-1). APVI explained a statistically significant proportion of cladoceran community variance whereas MPVI did not. RDA and associated forward selection indicated that the community, considered as a whole, was structured by three factors. In simple terms these factors represent food (Chla), predation (ZF) and living substrate or refuge from predation (PVI). Chla, however, had a relatively high variance inflation factor (VIF) (>4) (ter Braak & Šmilauer 2002) indicative of multi-colinearity and suggesting that of the variance attributed to Chla a high proportion of it was shared with other variables. The large co-variation terms associated with Chla in the partial RDA (Fig. 4-1) confirmed this, with more variance being uniquely apportioned to ZF and APVI.

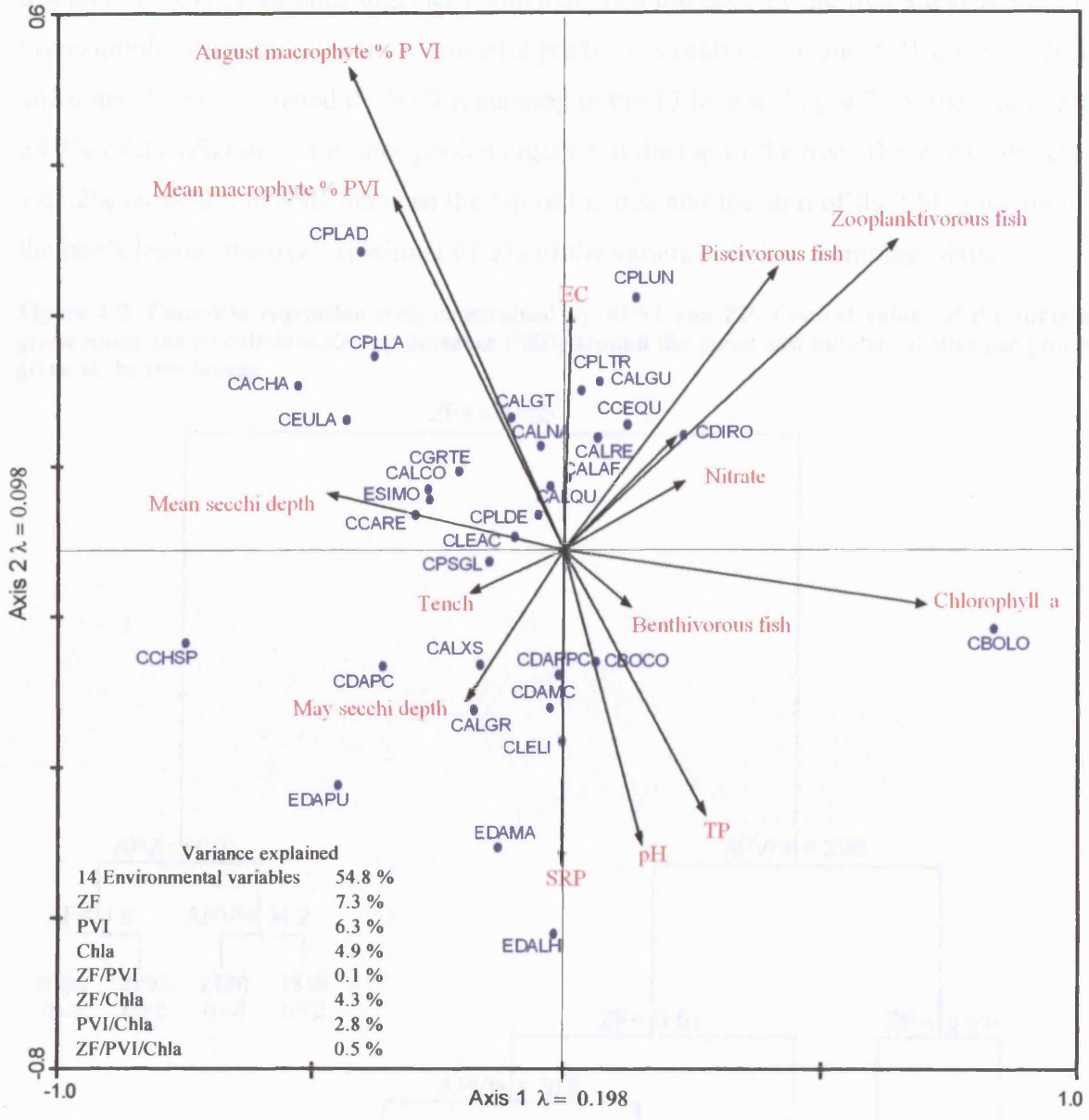
Table 4-2. Summary of summer minimum, mean and maximum values for key biological variables and percentage contribution to the surface sediment assemblage of key taxa at 39 sites. MPVI and APVI, BF (no. m^{-2}), ZF (no. m^{-2}), PF (no. m^{-2}) and cladoceran relative abundance for selected species.

							%	%	%	%	%	%
	MPVI	APVI	BF	ZF	PF	Tench	*B. longirostris*	*D. hyalina* agg.	*D. magna*	*Ceriodaphnia*	*A. harpae*	*C. sphaericus*
Min.	0	0	0	0	0	0	0.0	0.0	0.0	0.0	0.0	1.27
Median	13.7	6.8	0	0.44	0.02	0.01	33.0	15.9	0.0	14.3	0.0	20.75
Mean	16.3	13.8	0.004	0.71	0.02	0.11	38.1	18.9	4.5	19.5	2.3	35.49
Max.	45.7	58.8	0.1	3.26	0.15	2.94	91.8	69.2	43.5	82.7	14.7	70.71

Table 4-3. Correlation matrix of selected environmental variables from the 39 lakes. The values in bold are significant at P ≤0.05. Chla, TP, SRP, NO^{-}_{3}-N, Surface DO, MPVI, APVI, BF, ZF, PF, Tench & Mean SD.

	Chla	TP	SRP	NO^{-}_{3}-N	DO	MPVI	APVI	BF	ZF	PF	Tench
Chla	1										
TP	**0.53**	1									
SRP	0.26	**0.84**	1								
Nitrate	0.01	-0.06	0.02	1							
Surface DO	0.12	**-0.38**	**-0.38**	0.33	1						
Mean PVI	**0.37**	**-0.42**	**-0.31**	-0.15	-0.01	1					
August PVI	**0.30**	**-0.39**	**-0.30**	**-0.31**	-0.06	**0.82**	1				
Benthivorous fish	0.07	0.08	0.10	**0.35**	0.24	-0.20	-0.19	1			
Zooplanktivorous fish	0.30	-0.17	-0.38	0.06	0.10	0.13	0.07	0.07	1		
Piscivorous fish	0.10	-0.12	-0.17	0.20	0.16	0.17	0.19	-0.13	**0.34**	1	
Tench	0.18	-0.08	-0.15	0.05	-0.13	0.27	0.01	-0.17	0.15	0.05	1
Mean Secchi depth	**0.73**	**-0.60**	**-0.32**	0.05	0.15	**0.43**	0.25	-0.03	-0.17	-0.01	0.070

Figure 4-1. Biplot of RDA of surface sediment cladoceran assemblages of the 39 sites. Result of partial RDA are inset. Total variance due to the 14 variables and the % variance in the minimal adequate model unique to APVI, ZF and Chla are given.



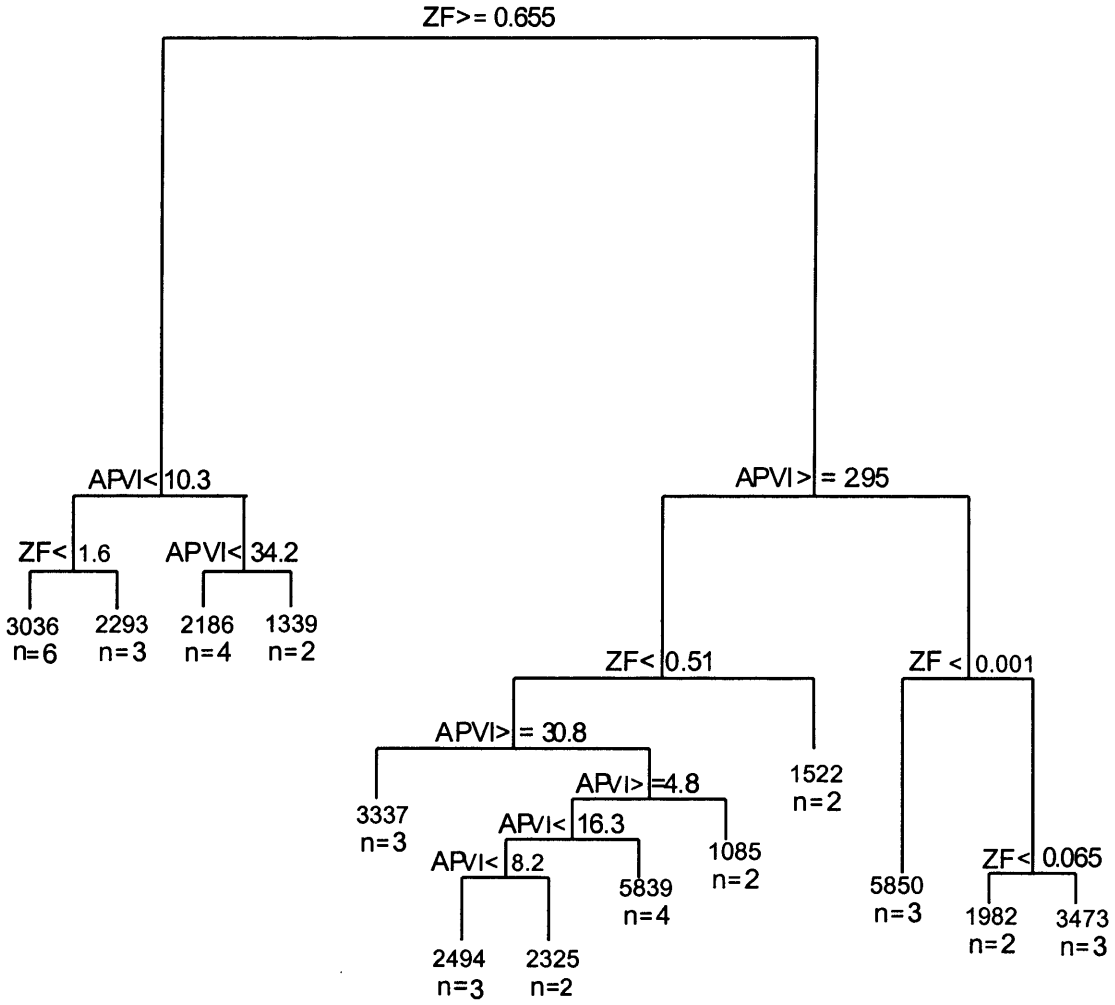
Taxa are (a) CACHA – *Acroperus harpae*; CALAF – *Alona affinis*; CALCO – *Alona costata*; CALGU – *Alona guttata*; CALGR – *Alona guttata/rectangula*; CALNA – *Alonella nana*; CALRE – *Alona rectangula*; CALQU – *Alona quadrangularis*; CALXS – *Alonella excisa*; CBOCO – *Bosmina coregoni*; CBOLO – *Bosmina longirostris*; CCARE – *Camptocercus rectirostris*; ECEQU – *Ceriodaphnia* spp.; CCHSP – *Chydorus sphaericus*; CDAPC - *Daphnia hyalina* agg. claw; CDAPCC – *Daphnia pulex* claw; CDAMC – *Daphnia magna* claw; EDALH – *Daphnia longispina/hyalina*; EDAMA – *Daphnia magna*; EDAPU – *Daphnia pulex*; CDIRO – *Disparalona rostrata*; CEULA – *Eurycercus lamellatus*; CGRTE – *Graptoleberis testudinaria*; CLELI – *Leydigia leydigii*; ELEAC – *Leydigia acanthercoides*; CPLAD – *Pleuroxus aduncus*; CPLUN – *Pleuroxus uncinatus*; CPLDE – *Pleuroxus denticulatus*; CPLLA – *Pleuroxus laevis*; CPLST – *Pleuroxus striatus*; CPLTL – *Pleuroxus trigonellus*; CPLTR – *Pleuroxus truncatus*, CPSGL – *Pseudochydorus globosus*; ESIMO – *Simocephalus* spp.

4.4.2 Regression trees

The recursive partitioning procedure, or MRT analysis, employed to model the assemblage-environment relationship produced a tree with 13 "leaves" explaining 66.8% of the species

variance when all environmental variables were included in the model. The amount of variance explained was calculated by the reduction in the sum of squared Euclidean distances (SSD) of all sites together compared with the SSD of the tree's leaves summed. For example, when only the most powerful predictor variables, ZF and APVI, were selected and a new tree constructed the SSD remaining in the 13 leaves (Fig. 4-2) of the tree totalled 38.8% of the SSD of all the sites pooled together at the top of the tree. There was, therefore, a 61.2% reduction in SSD between the top of the tree and the sum of the SSD remaining in the tree's leaves, the tree explaining 61.2% of the variance in the assemblage data.

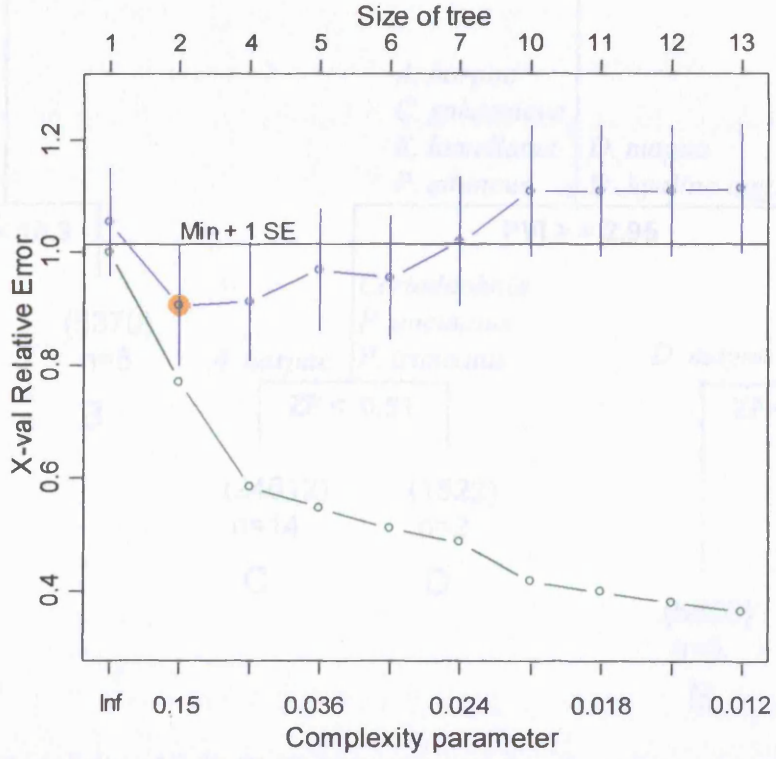
Figure 4-2. Complete regression tree, constrained by APVI and ZF. Critical values of the splits are given where the tree divides. Group deviance (SSD) around the mean and number of sites per group is given at the tree leaves.



As MRT tends to over-fit the model to the data, leading to a tree with little predictive accuracy (Breiman et al. 1984), cross-validation was employed to strike a balance between explanatory and predictive power. The best predictive model based on the cladoceran data

had only two leaves (Fig. 4-3) and was therefore of limited ecological use. Thus, the 1-SE rule was applied (Breiman et al. 1984), i.e. the most complex tree within 1 SE of the "best" predictive tree, with a complexity parameter of 0.03 (Fig. 4-3) and six leaves was selected as the optimal vehicle for prediction. The resulting tree (Fig. 4-4) explained 48.8% of the community variance. The first split reduced the SSD by the greatest amount, and was conditional upon ZF abundance >0.655 fish m^{-2}. *Daphnia* and *C. sphaericus* were significantly associated with lower fish density and *B. longirostris* with values >0.655 fish m^{-2}. The second tier of the partition was based on APVI. As in RDA (Fig. 4-1), APVI data rather than the summer mean value based on June and August sampling was selected as the variable best explaining the variance in the cladoceran data. At higher ZF values, relatively high APVI >10.3% was responsible for the split of groups A and B, whereas at low ZF levels, the mere presence of plants, APVI >2.95%, was sufficient to cause a significant difference in the cladoceran assemblage.

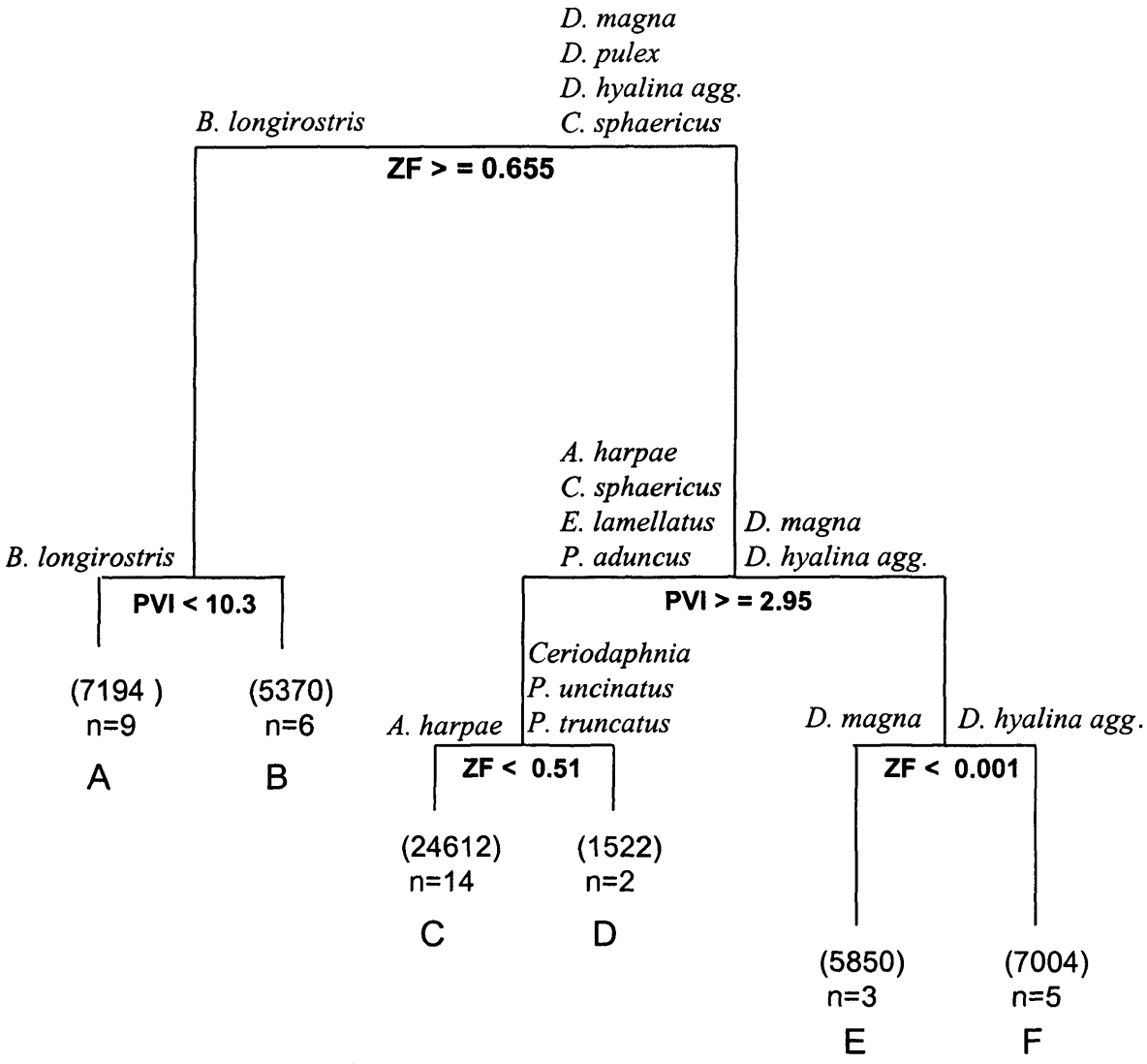
Figure 4-3. Cross-validation of the regression tree showing the explanatory power (lower line) and predictive power (upper line) and the distance of one standard error from the best model (solid horizontal line). The circled point is the model with the greatest cross-validated predictive accuracy.



Species significantly (P <0.05) associated with the presence of aquatic macrophytes in August, at lower fish densities were *A. harpae, E. lamellatus, C. sphaericus* and *P. aduncus*. Groups C and D with APVI >2.95% and ZF <0.655 no. m^{-2} were divided by ZF

>0.51. Group C had no unique indicator species, *A. harpae* was, however, associated with the lower ZF part of the split (Fig. 4-4). Species significantly associated with group D were *Ceriodaphnia* spp., *P. uncinatus* and *P. truncatus*. Group E and F had low ZF and low APVI and were separated by ZF <0.001 no. m^{-2}, i.e. the presence or absence of fish. *D. magna* was a significant indicator species for group E and *D. hyalina* agg. for group F.

Figure 4-4. Pruned regression tree, the first split places sites with ZF >0.655 no. m^{-2} ZF to the left and ZF <0.655 no. m^{-2} to the right. Indicator species which were significantly (P <0.05) associated with the split are placed on the relevant side of the split. The final leaf or MRT-group (A-F) SSD is given (in brackets) as is the number of sites per group (n=x).



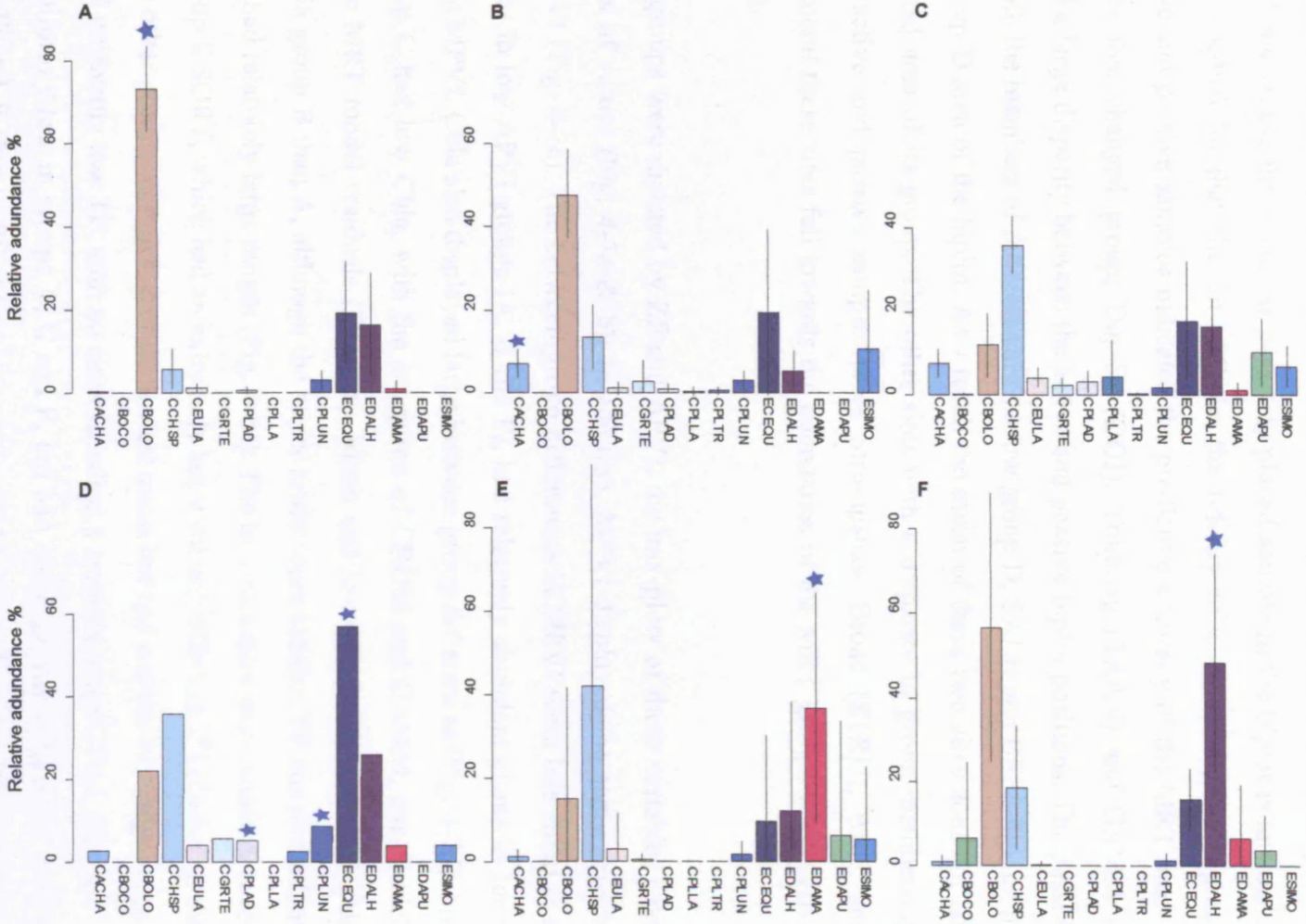
The ANOSIM R statistic of 0.53 (P <0.001) suggests that there were significant differences in community composition between the six MRT designated groups. There was a relatively large difference in the within-group SSD (Fig. 4-4), standardised by the number of sites within the group. Groups A, B and D displayed a lower SSD (799, 895 and 761,

respectively), whereas groups C, E and F showed much greater within-group heterogeneity (1758, 1950 and 1400 respectively).

The mean relative abundance of selected species and their 95% confidence limits provide an illustration of the difference in community composition of the regression tree groups (Fig. 4-5). There were a number of ubiquitous species, such as *C. sphaericus* and *D. hyalina* agg, which although present in all groups, occurred in very different proportions within each group. *B. longirostris* was present in large proportions in both groups A and B. A number of plant-associated species, including *Simocephalus* spp. and the indicator species *A. harpae* separated group B from A. Group C was characterised by high species richness and the most evenly distributed assemblage with no one species dominating the community. The group contained several plant-associated species, including *E. lamellatus, G. testudinaria* and *P. laevis*. Group D contained a number of indicator species, including the intermediate-sized pelagic species *Ceriodaphnia* spp. and the plant-associated *P. aduncus*. Groups E and F were dominated by planktonic species (*Daphnia, Bosmina,* and *Ceriodaphnia*) and the behaviourally plastic, semi-planktonic *C. sphaericus* (Fryer 1968). Groups E and F were separated by the co-dominance of *D. magna* and *C. sphaericus* where ZF were absent in group E as opposed to the combination of *D. hyalina* agg. and *B. longirostris* in group F where fish were present.

There were a number of differences in the proportions of pelagic species between the groups. The high ZF group A had similar or higher abundances of *D. hyalina* agg. than group B and a comparable mean number of *Ceriodaphnia* spp. Group B had higher within-group variability as reflected by wide confidence limits. *D. pulex* agg. occurred only at very low ZF (E and F) or at low ZF in the presence of plants (C). The slight increase in ZF density between groups C and D resulted in the absence of *D. pulex* and an increase in the proportion of *Ceriodaphnia*. *C. sphaericus* also occurred in higher proportions where plants were abundant and/or ZF was low (C, D, E and F)

Figure 4-5. Bar-plot of the mean species relative and weighted relative abundance and 95% confidence limits for the six multiple regression tree (MRT) groups A-F. Taxa are (a) CACHA – *Acroperus harpae*; CBOCO – *Bosmina coregoni*; CBOLO – *Bosmina longirostris*; CCHSP – *Chydorus sphaericus*; CEULA – *Eurycercus lamellatus*; CGRTE –*Graptoleberis testudinaria*; CPLAD – *Pleuroxus aduncus*; CPLLA – *Pleuroxus laevis*; CPLTR – *Pleuroxus truncatus*; CPLUN – *Pleuroxus uncinatus*; ECEQU – *Ceriodaphnia* spp.; EDALH – *Daphnia hyalina* agg.; EDAMA – *Daphnia magna*; EDAPU – *Daphnia pulex*; ESIEX – *Simocephalus* spp. Star denotes group indicator species determined by INDVAL.



4.4.3 MRT Model evaluation

RDA with the sites both active, i.e. constrained by their measured ZF and PVI values, and passive, placed within the constructed model solely according to their sub-fossil cladoceran assemblage, provided a means with which to assess the "fit" of the MRT model (Fig. 4-6). The distance between the fitted and the passively placed sample in the biplot is analogous to the model residual for that site. In addition, the fidelity of a site to the MRT group between active and passive samples indicated the predictive accuracy of the MRT model. Of the 8 sites that changed group; Døj Sø (DOJ), Tranevig (TRAN) and GAMM in particular had a large disparity between the active and passive biplot positions. The passive samples of both the members of the relatively narrow group D, SALH and BEES did not lie within the group D area of the biplot. As a result the mean of these two sites does not fall within the fitted area of its group. The other sites with a disparity in group membership between the active and passive samples were Strumpshaw Broad (STRU), BLIC and CROM. In general these sites fell towards the boundaries of the MRT groups when active in the analysis.

As the MRT groups were dictated by ZF and APVI, the box-plots of these variables have distinct ranges of values (Fig. 4-7a & b). In addition, MPVI displayed the same general pattern as APVI (Fig. 4-7c). The between-group differences in MPVI were less sharp as a number of sites in low APVI groups (A, E and F), had relatively abundant plants in June, thus increasing MPVI. Chla also displayed large between group differences (Fig. 4-7d). For example, group C had low Chla, with the exception of CROM and GAMM, sites which both had large MRT model residuals (Fig. 4-6). Mean and lower quartile values of Chla were smaller in group B than A, although the upper limits were similar. TP concentrations for all groups had relatively large ranges (Fig. 4-8e). The box-plot does not contain data for one site in group E SORT, which had an extremely large value (>3000 $\mu g\ l^{-1}$) obscuring the patterns in the other groups. Group C had the lowest mean but had a relatively large range, whereas B had uniformly low TP, with no site exceeding a summer mean TP of ≈90 $\mu g\ l^{-1}$. Nitrate was uniformly low in groups B, C and F, but had much greater ranges and means for groups A, D and F (Fig. 4-8f). Mean summer and August values for SD had fairly characteristic patterns indicated clearer water in groups B and C. The mean summer signal may be complicated by generally 'turbid' lakes having clear-water phases in the spring (Scheffer et al. 2001). The maintenance of high water clarity in August provides a more

marked separation of the groups. Sites in groups A and F had generally turbid water by August, whereas in groups B, C, D and E sites had generally higher August SD. In group C, although the mean of August SD was high, there was a large range, with a number of sites with very low August SD. GAMM, DOJ and CROM lowered the overall mean. Without exception these sites failed to remain in group C when their samples were passively placed in the RDA (Fig. 4-6).

Figure 4-6. RDA biplot of sedimentary cladoceran assemblages from the 39 lakes constrained by APVI and ZF. Each site is placed actively giving a fitted value (red cross ✖) and passively, giving an unfitted value (blue circle ●). The distance between the fitted and passively placed sample approximates the models residuals. The MRT group mean is also placed passively. The MRT delimited groups are separated by their critical values. Sites changing MRT group between active and passive sample have an arrow showing their trajectory.

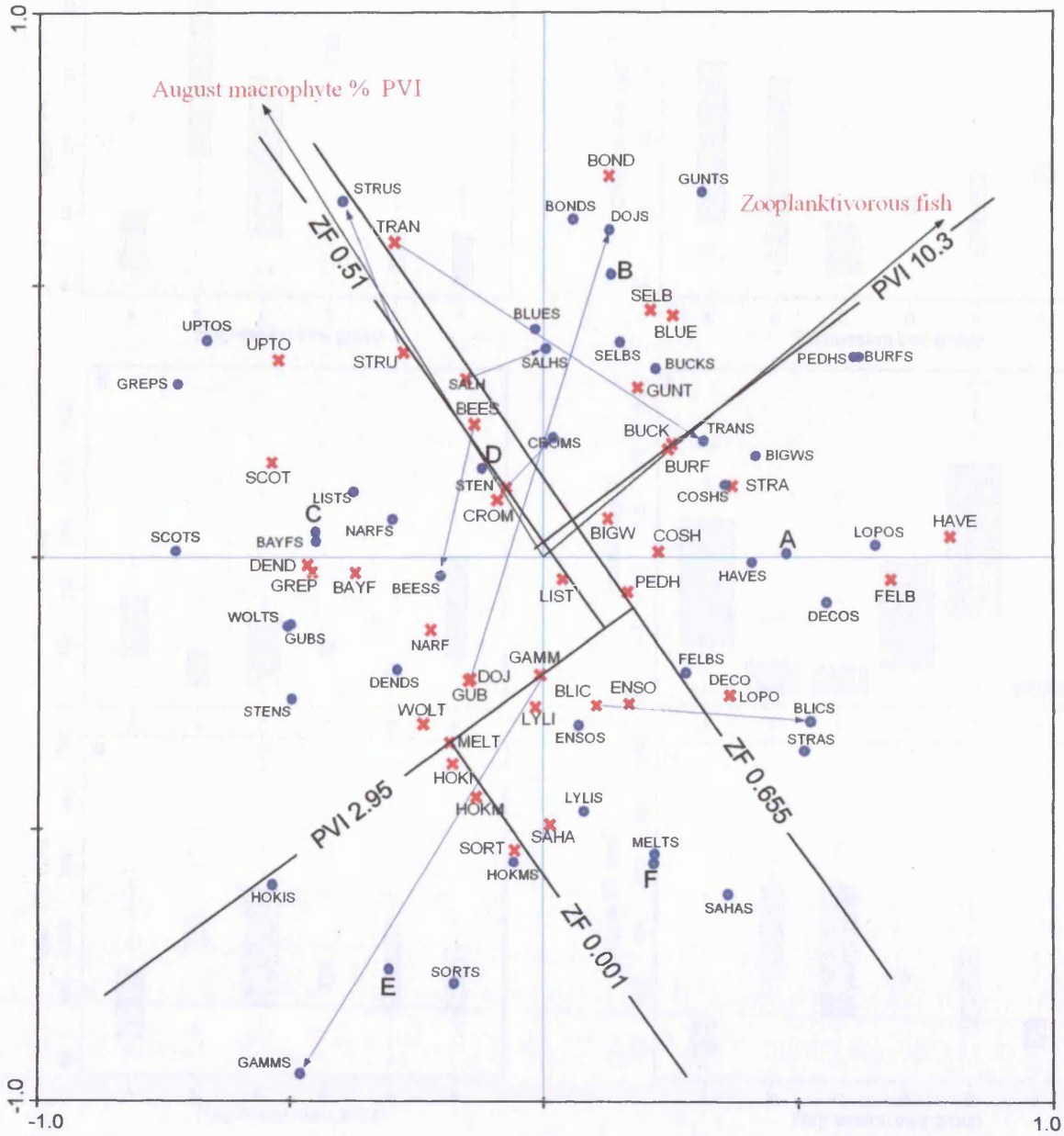
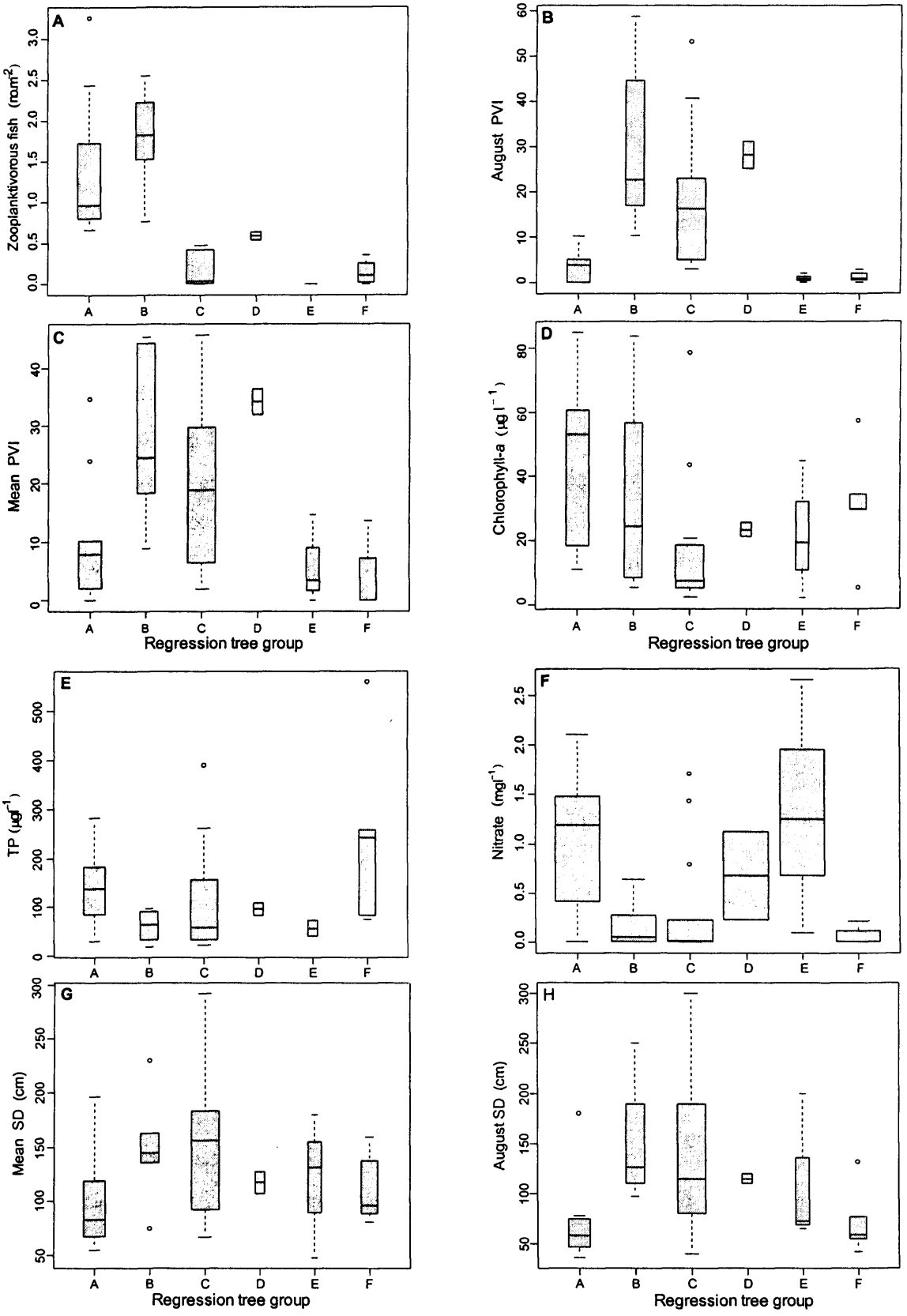


Figure 4-7. Box plots of the group environmental variables A) ZF, B) APVI, C) MPVI, D) Chla, E) TP excluding SORT, F) Nitrate, G) mean SD, H) August SD.



4.5 Discussion

4.5.1 MRT performance

Multivariate regression tree (MRT) analysis produced a model where two parameters (ZF & APVI) had comparable explanatory power to RDA employing 14 environmental variables, a similar phenomenon to that seen in previous studies (De'ath 2002). In keeping with the RDA, in the most parsimonious MRT, as derived by cross validation, ZF and APVI best predicted community change. This accorded well with previous work on both contemporary and surficial-sediment cladoceran communities in shallow lakes (Timms & Moss 1984, Schriver et al. 1995, Jeppesen et al. 2003a, Chapters 2 & 3). The very large proportion of the variance explained by two variables in the MRT analysis may result from the method allowing for variation in the strength of the structuring forces along the trophic gradient, for linear and non linear responses and for higher order interactions. As with almost any classification it could be argued that the groups delimited by the MRT are artificial constructs of the model. The results, however, suggest that there are critical values, within this data set, of ZF and APVI which are 'break points' of ecological function and result in significantly different cladoceran assemblages.

There were clear differences in cladoceran assemblages between the groups, the statistical significance of which was confirmed by ANOSIM. The difference in the groups was driven, to a large degree, by direct relationships between the sub-fossil assemblages and ZF and APVI. In general it is desirable for a model to be based on causative mechanisms (Guisan & Zimmerman 2000). It is inevitable, however, that in shallow lakes, where the causes and effects of change are strongly linked and inter-dependent (Jeppesen et al. 2000), that ZF and APVI summarise additional variation in the cladoceran assemblage which they may not directly cause. Thus, they become a 'proxy' for the effects of several factors, including TP, nitrate, Chla, SD and benthivorous fish density. The relationship of these other variables with the cladoceran community may be direct, as in Chla, which as a measure of food-availability directly affects the assemblage (Vanni 1987), or indirect through modification of the predator-prey relationship by affecting water clarity (Diehl 1988, Breukelaar et al. 1994, Gliwicz 2002, Chapter 2). Although the model does not

contain them as predictors, the MRT defined groups also summarise between-group differences in TP, Chla, nitrate, MPVI and SD.

The greater statistical significance of APVI over MPVI in explaining the variation in the cladoceran assemblages in both the RDA and MRT analyses may, similarly, be attributable to APVI summarising community change that macrophyte abundance may not directly cause. Macrophyte abundance has direct effects on cladoceran community composition (e.g. Whiteside 1970), providing habitats for plant-associated species and refuge from predation for pelagic cladocerans (Wright & Shapiro 1990). Furthermore, submerged macrophytes play a key role in the structure and function of lake ecosystems, having direct and indirect effects on a range of physical, chemical and biological patterns and processes (Carpenter & Lodge 1986, Diehl 1988, Dieter 1990, Jeppesen et al. 1997a). At a number of sites sampled in this study there was a 'crash' in PVI between June and August. The persistence of submerged macrophytes until August appears to both shape and reflect lake ecological function. Two sites, with high PVI (>30%) in June, were placed in group A (turbid, high ZF, low PVI sites) as their macrophyte populations abruptly declined to zero by August resulting in turbid water and low SD in August. These sites had cladoceran assemblages more typical of turbid sites, where plants are completely absent, than clear water sites, where plants persist to late summer. Thus, the cladoceran community, although partially driven by a direct plant PVI-assemblage relationship, additionally appears to be a reflection of whole ecosystem function. The MRT defined groups, therefore, although designated purely on the grounds of their APVI and ZF, may describe distinct forms of ecological structure and function.

4.5.2 MRT group ecological function

The MRT groups appear to reflect the changes in both ecological structure and function associated with the manifold effects of nutrient enrichment (Jeppesen et al. 2000). Groups B, C and D contained clear water sites with generally abundant aquatic plants, despite large differences in ZF density. Group C had the highest proportion of benthic cladoceran species. At the majority of sites this was the result of abundant macrophyte cover (Lauridsen et al. 1996), although a few sites, e.g. NARF and Listrup Lyng (LIST), had relatively low PVI and clear water and therefore primary productivity was probably predominantly due to benthic algae at the sediment surface (Liboriussen & Jeppesen 2003).

The shift to a greater proportion of *Ceriodaphnia* spp. relative to the larger *Daphnia* species and higher Chla in group D suggested a more pronounced cascading effect of ZF and perhaps an increase in the proportion of planktonic primary production. Groups B and D had generally higher APVI than group C, suggesting that higher plant abundance is required to maintain relatively clear water conditions as ZF densities increase (Wright & Shapiro 1990). Although precise values of one parameter may be misleading, given that many other factors may also be important, PVI values for groups B and D are around the 30% estimated by Jeppesen et al. (1994) as necessary to maintain clear water conditions. This can perhaps be further qualified as the PVI required to maintain clear-water conditions at ZF abundance above ≈0.6 no. m^{-2}. The range of Chla within group B indicates that at some sites the effects of ZF predation on the cladoceran community resulted in increased phytoplankton crop. Furthermore, these data may indicate the importance of bottom-up forces. There was no direct quantifiable link evident between nutrients (TP and nitrate) and ecological function when all the sites were considered together. Within group B, however, TP and nitrate concentrations were relatively low (TP <100 $\mu g\ l^{-1}$, nitrate <0.28 mg l^{-1}), suggesting that clear-water conditions may only be attainable at high fish densities where nutrient levels are low.

Groups A, E and F were dominated by planktonic production. The differences between the groups were chiefly a reflection of ZF density. The sites in group A were turbid, occupying the phytoplankton-dominated stable state. In keeping with the alternative stable state theory (Scheffer et al. 1993) these turbid sites had a large range of TP, plants were rare or absent, and ZF density was high. Where plants did persist in group A they were generally the water-lilies (*Nymphaea alba* L. and *Nuphar lutea* L.), which are typically persist at higher turbidity than other more sensitive species. Sites in groups E and F had very low ZF abundance with fish communities either dominated by species such as large carp Holkham Hall lake main section (HOKM) and BLIC, or larger individuals of rudd (*Scardinius erythropthalamus* L.), (LYLI), larger roach (SAHA) or just the absence of zooplanktivorous species (MELT and SORT). There may be many reasons for these low ZF densities such as site isolation or fish kills resulting from low oxygen, likely to have occurred at SORT and SAHA. The outcome is a fairly similar form of ecosystem function, in groups E and F to that in group A, despite very different ZF density, with planktonic production dominating over benthic production. It is interesting to note that, despite the

dominance of planktonic production in all three groups, only sites in group F suffered from blue green algal blooms, perhaps as a result of high herbivorous grazing pressure or low concentrations of nitrate (Ferber et al. 2004).

The difference in within-group heterogeneity (SSD), standardised by the number of sites within the group, was most likely a product of variation in community composition within groups C, E and F that was not attributable to APVI or ZF. In group C, although variation of APVI within the group will partly explain the larger within-group SSD, Chla and invertebrate predation (Goulden 1981, Scheffer 2000) may also cause some between-site differences. Similarly, in group E and F it may have been dissolved oxygen, concentrations of which varied greatly, rather than ZF and APVI that caused the high within-group heterogeneity.

Recent research has identified a loss of benthic pathways of production as a broad scale response of shallow lakes to nutrient enrichment (Vadeboncoeur et al. 2003). At very low nutrient levels the majority of primary production being benthic, either via macrophytes or attached forms of algae (Moss et al. 2003). As nutrient levels rise the importance of benthic production declines and that of phytoplankton increases. The MRT groups appear to identify such a shift with groups B, C and D having varying, but significant, amounts of benthic primary production. In contrast, the sites in groups A, E and F were almost exclusively dominated by planktonic forms of production. At these sites where benthic species of cladoceran were present, for example at SORT, it is likely they were feeding on detritus settled out from the plankton. Thus, analysis of cladoceran communities may elucidate changes in ecological function that analysis of other parameters may miss. For example, increased phytoplankton production may not result in higher Chla if herbivory increases, but it would lead to greater abundances of planktonic cladocerans. Thus, whilst ecological structure and state may remain stable, ecological function may change relatively smoothly as benthic production gives way to planktonic production (Vadeboncoeur et al. 2003). This shift in the balance productivity is reflected, to some degree by a sites MRT group membership and also perhaps by the relative position of a site in the RDA biplot (Fig. 4-6).

4.5.3 Model assessment

When the model was inverted and the sedimentary assemblages were passively laid in the RDA 8 of 39 sites (20.5%), were misclassified in what amounts to a fairly liberal test. Rather than discredit the model as a means of reconstructing past trophic structure and function, however, it may actually be illustrative of the sensitivity of cladoceran communities to ecosystem change and hence the advantages of palaeolimnology. Surface-sediment samples are a combination of remains from between 1-5 years, and thus inter-annual variation is incorporated into the assemblages. Shallow eutrophic lakes may display relatively large inter-annual variability in ZF (Cryer et al. 1986, Perrow et al. 1999) due to instability of a skewed population dominated by small young fish. In addition plant-dominated sites may have significant inter-annual variation in macrophyte community structure (Capers 2003), and even abundance, perhaps in response to increased planktonic productivity (Blindlow et al. 1993). Thus, the calibration of a sedimentary assemblage against environmental data from a single year may contain some error if conditions varied significantly in the preceding years. For example, the misclassification of BLIC may have been due to cycles in ZF density. BLIC had relatively high TP, very high Chla and no submerged plants, conditions under which inter-annual variation in ZF tends to occur (Cryer et al. 1986). Examples of where the surficial-sediment assemblage was misclassified by the calibrated model but verifiably performed well were CROM and DOJ. Both sites experienced fish kills either during the sampling period prior to fish sampling in late summer. The surface-sediment assemblage was, therefore, predominantly deposited at higher ZF density than was measured in the fish survey. The fitted values fell into class C, owing to lower fish, but the passive sample reflected the higher ZF present previous to the fish kill, placing it in group B. The most pronounced shift occurred at DOJ, where the surface sediments indicated much higher ZF density than was actually observed.

The summer mean Chla for CROM, which was very high for group C was skewed by the higher values prior to the fish kill. The other very high Chla value in group C belonged to GAMM, another site that changed group between active and passive samples in the RDA model test. Despite a small patch of white water lily, GAMM functioned in the same way as other plant-free sites with frequent blue green algal blooms and high Chla. Thus, the constrained sample for GAMM does fit with the clear-water conditions of group C. The passively placed sample apparently reflects the ecological function of the lake more

accurately, as the presence of some plants constrained the site in group C. In addition at GAMM ZF density is relatively high, but dominated by large rudd, which probably feed more extensively on larger invertebrates. Thus, the actual predation pressure exerted on the zooplankton community may have been less than the data suggest.

The other sites that failed to remain in their MRT designated groups between fitted and passive samples STRU, SALH and BEES all had relatively small residuals and were situated near the boundary of their group. The one true failure of the method was TRAN which moved from group A to B equating to the shift between stable states. TRAN was an unusual site having extremely shallow brown water with high turbidity, both suspended sediment and Chla, but where aquatic plants, chiefly the tolerant *Ceratophyllum demersum* L., persisted and had high APVI. It therefore had relatively unique conditions within the training set. Thus, overall it can be argued that the model only truly misclassified one site out of a total of 39.

4.5.4 Spatial and temporal integration of remains

In most cases the between-group differences in species incidence, as reflected by sedimentary remains, was in keeping with findings from studies of contemporary cladoceran ecology. For example, the proportion of plant-associated species was larger in the groups with aquatic plants (B, C and D) (Lauridsen et al. 1996) and large bodied pelagic species dominated sites with very low fish predation pressure, in particular groups E and F where plants were uncommon (Lauridsen & Lodge 1996). Furthermore, size selective predation on those larger species allowed the relative abundance of *B. longirostris* to rise in concert with ZF density, reflected in its abundance in groups A and B and despite much lower absolute ZF density, in group F (Brooks & Dodson 1964).

There were cases, however, when between-group similarities agreed less well with known contemporary cladoceran ecology. A striking example is the relative parity of the mean weighted relative abundance of *D. hyalina* agg and *Ceriodaphnia* spp. ephippia between groups A, B and C, in spite of very different fish and plant densities, which should result in distinct communities of both pelagic and benthic species (Timms & Moss 1984, Wright & Shapiro 1990, Lauridsen et al. 1996). This divergence from the expected patterns may result from the fact that surface sediments are an accretion of remains from between 1-5

years and are, therefore, spatial and temporal integrations of contemporary cladoceran communities (Vanderkerkhove et al. 2005). Thus, seasonal differences in species occurrence reflecting distinct ecological processes may not be obviously apparent from sedimentary assemblages. For example, turbid sites, such as those in group A, generally have a fish community dominated by small zooplanktivorous species (Jeppesen et al. 2000) which often do not successfully over-winter, resulting in a comparatively low ZF density in spring (Perrow et al. 1999). This seasonal instability may lead to low fish predation pressure in April and May, which combined with abundant phytoplankton, allows the proliferation of *Daphnia* spp., perhaps leading to a spring clear-water phase (Lampert et al. 1986, Scheffer 2001). Subsequently, young of the year, or recently spawned, fish are recruited to the population in early summer, typically June, and begin selectively feeding on larger cladocerans. Thus, these sites may experience intense fish predation pressure in the summer but very low predation pressure in early spring, in such sites *Daphnia* are typically absent by late summer (Stansfield et al. 1997). As fish numbers increase in spring, and conditions become less favourable, *Daphnia* may sexually reproduce and ephippia are produced. Conversely, in clear-water sites, such as those in group B, fish populations tend to be more stable, characterised by smaller numbers of larger individuals. ZF predation does not display such large seasonal variation and nutrient levels are generally lower. Clear water conditions are maintained throughout the growing season (as in group B and C) and *Daphnia* spp. are present throughout the summer (Chapter 2). Ephippia production tends to occur when conditions become less favourable at the end of the summer as temperatures and food availability decline. Thus, the distinct ecological functioning of groups A, B and C can result in similar abundances of ephippia in the sediments. The remains, however, may have been deposited in different seasons and as a result of distinct ecological processes, resulting from changes in macrophyte abundance and ZF density. Thus, it may be impossible to establish a reliable, precise quantifiable relationship between sedimentary remains of one species and ZF density along a gradient where there are significant shifts in ecological function. Indeed, only when the entire community is considered can the abundance of these remains be placed in a meaningful context.

4.6 Conclusions

Palaeoecological inference models have traditionally reconstructed one value in isolation from a training set of sites which shows variation in a number of variables important in shaping the communities. Thus, the error involved in the prediction may be non-random. Where there are non-linearities or hysteresis in species and ecosystem responses to the changing environment this can result in extremely poor prediction of past conditions. In addition the integration of seasonal and inter-annual variability by surface sediment assemblages must be taken into account in order to explore fully the sub-fossil-environment relationship. This is illustrated, in this study, by the fact that even the strongest, least complex relationship, such as that between *D. magna* and ZF density (Chapter 2), does not show the seasonal or inter-annual consistency between sites along the length of the trophic gradient. Thus, a prediction of the *D. magna* ephippia abundance at a given ZF density cannot be achieved with any confidence.

The data analysed here and in Chapters 2 and 3 strongly indicate that no single cladoceran species can be employed to model the changing environment within a data set of 39 shallow lakes. Thus, a species-driven but community-based approach was employed to identify critical points in ZF and APVI where surficial-sediment cladoceran assemblages changed. These shifts in community composition, although chiefly driven by ZF and APVI appear to reflect differences in ecosystem function associated with nutrient enrichment, in particular the shift in ecological function as the benthic pathways of production are eroded and pelagic productivity increasingly dominates (Vadeboncoeur et al. 2003). As such, when applied to core material, the model represents a robust technique capable of reconstructing shallow lake ecological structure and function. In contrast to the transfer function approach this technique does not predict absolute values but provides a range of probable values and an assessment of relative temporal change. Thus, it is more ecologically relevant and robust allowing for the inherent noise in biological data shaped by multiple interacting factors and based on a sample of the population. In addition, the method appears sensitive to relatively small changes in ZF (group C and D to B and A respectively) and the presence and absence of a significant abundance of submerged macrophytes. Thus, it may allow the sequencing of events associated with eutrophication related changes in ecological function and the loss

of submerged macrophytes in shallow lakes. It may prove particularly powerful in combination with other techniques that reconstruct different elements of the shallow lake food-web such as plant macrofossils (Davidson et al. 2005) and algal pigments (Leavitt et al. 1994), providing a fuller picture of temporal change in response to eutrophication at all trophic levels.

5 Chapter 5 - Tracking change in shallow lake structure and function: The simultaneous reconstruction of zooplanktivorous fish density and macrophyte abundance from fossil cladoceran assemblages.

5.1 Introduction

It is probable that very few aquatic systems are un-impacted by human activity (Wetzel 2001, Smol et al. 2005). Shallow lakes in lowland catchments, in particular, are likely to have a long history of human influence. Indeed many are artificial and thus their origins are a result of human activity. In the absence of long-term monitoring data the remains of plants and animals preserved in lake sediments may allow insights into a lake's past physical, chemical and biological conditions (Anderson & Battarbee 1994). Palaeolimnological techniques can provide information on former biological communities and ecosystem response to environmental change (Smol 1992). Such data facilitates not only the determination of pre-disturbance assemblages but may also elucidate the nature of community response to disturbance over timescales normally inaccessible to contemporary investigations (Battarbee et al. 2005).

Lake ecosystems have been impacted by a number of different human activities with perhaps the most pervasive being eutrophication. Experimental and empirical studies have demonstrated that the response of shallow lakes to eutrophication is complex, characterised by hysteresis and regime shifts (Irvine et al. 1989, Moss 1989, Scheffer et al. 1993, Jeppesen et al. 2000). Thus, whilst increased nutrient levels are the driving force behind eutrophication, ecosystem state or regime is not solely dictated by epilimnetic nutrient concentrations (Scheffer et al. 1993).

A number of studies have used biological remains in lake sediments to track shifts in shallow lake ecosystem structure and function in response to eutrophication (Sayer et al. 1999, Brodersen et al. 2001). In addition several transfer functions have been developed to

infer quantitatively past chemical and biological conditions in shallow lakes (e.g. Bennion et al. 1996, Brodersen et al. 1998, Jeppesen et al. 1996, 2001, Amsinck et al. 2005). Despite the impressive performance diagnostics, the predictive accuracy of models employing the transfer function approach has increasingly come into question (Jeppesen et al. 2001, Velle et al. 2005, Battarbee et al. 2005a), particularly in shallow lakes (Bennion et al. 2001, Sayer 2001). Sedimentary cladoceran assemblages have been shown to respond to changes in the ecological structure and function resulting from changing trophic status (Hoffman 1996, Hann et al. 1994, Amsinck et al. 2003) and fish addition and removal (Leavitt et al. 1989). Thus, they have great potential for tracking changes in ecosystem structure and function. Yet the multiple forces structuring the sub-fossil cladoceran assemblage (Chapters 2, 3 and 4) and the fact that sedimentary remains are temporal integrations of contemporary populations (Vandekerkhove et al. 2005) preclude the use of a traditional transfer function approach (Chapter 4).

This study represents the first application, in freshwaters, of an inference model capable of the simultaneous reconstruction of two variables. The technique is based on the application of a multivariate regression tree (MRT) based model which places a sub-fossil assemblage in one of six groups corresponding to a range of zooplanktivorous fish density and August macrophyte abundance. Thus the method provides semi-quantitative estimates of past zooplanktivorous fish density and macrophyte abundance (Chapter 4). The semi-quantitative nature of the model allows for the inherent noise in biological data. The model is applied here to sub-fossil cladoceran assemblages from sediment cores from two shallow lowland lakes. It reconstructs eutrophication-related temporal variation in the ecological structure and functioning associated with shifts in fish and macrophyte abundance.

In addition to cladoceran remains, plant macrofossils were analysed from cores from the same two sites. Sedimentary remains left by the aquatic plants have been shown to track accurately changes in the dominant component of submerged vegetation (Davidson et al. 2005). These data, therefore, provide an independent assessment of shifts in the aquatic flora of the sites and therefore, in combination with historical information on past fish populations for the sites, the supplementary data allow a partial validation of the reconstruction approach and an assessment of its veracity.

5.2 Study sites

5.2.1 Kenfig Pool

Kenfig Pool (SS 790 820) is a shallow (max. depth 260 cm) moderately large (24 ha) lake situated within the extensive sand-dune system of the Kenfig National Nature Reserve, alongside Swansea Bay, south Wales and is thought to be around 7,500 years old, being created in association with sand-dune formation in Swansea Bay (Giles 2003). The geology is base-rich consisting of limestone and marine-derived sands.

Kenfig Pool has, for a shallow lake, relatively low nutrient levels with annual mean TP of 27 $\mu g\ l^{-1}$, chlorophyll-*a* (Chla) of 8.9 $\mu g\ l^{-1}$, annual mean conductivity of 314 $\mu S\ cm^{-3}$ and relatively high alkalinity of 102 mg l^{-1} $CaCO_3$ (Environment Agency (EA) 2003-2004 unpublished data). The site is noted for its aquatic macrophyte flora and is an important conservation resource. It was designated as a Site of Special Scientific Interest in 1953, a National Nature Reserve in 1989 and is currently a candidate Special Area of Conservation (cSAC) for hard-water oligo-mesotrophic waters with benthic vegetation of *Chara* formations. The open-water macrophyte community includes: *C. demersum*, *Ranunculus circinatus* Sibth., *Myriophyllum spicatum* L., *Potamogeton crispus* L., *Potamogeton lucens* L., *Potamogeton pectinatus* L., *Potamogeton trichoides* Cham. & Schlecht., *Littorella uniflora* L., *Chara aspera* Deth. ex Wild., *Nitella flexilis* L. and along the sandy shore section, the aquatic moss *Fontinalis antipyretica* Hedw. (ENSIS 1996).

Kenfig Pool is a valued resource for anglers and has been the subject of fish stocking for at least 50 years, with anglers' records dating back to the beginning of the 20th century (Giles 2002). There are detailed records of fish additions dating back to the first documented stocking episode in 1957.

5.2.2 Felbrigg Lake

Felbrigg Lake (TG 191 388) is a shallow (max. depth 150 cm), small (2.7 ha), lowland 'estate' lake, in the grounds of Felbrigg Hall, North Norfolk. It formed part of the 'training set' of 39 sites from which the model applied here was developed. Its origins were as a number of small 'stew ponds' stocked with carp and tench in the 17th century. These ponds

were subsequently amalgamated and the lake expanded and has existed in its current form since approximately 1843 (Maddison 1995). The catchment geology consists of Neogene and Pleistocene sand overlain with fluvioglacial and aeolian drift.

The lake has both high conductivity (summer mean 510 μS cm^{-3}) and alkalinity (summer mean 142 mg l^{-1} $CaCO_3$). It is currently eutrophic (OECD 1992) with a summer mean Chla of 18 μg l^{-1}, TP of 139 μg l^{-1} of which SRP is 30 μg l^{-1} and nitrate is 1.2 mg l^{-1} (Sayer & Davidson unpublished data). A number of macrophyte species namely, *Potamogeton pusillus* L., *P. pectinatus*, *P. crispus* and *Zanichellia palustris* L., associated with higher nutrient levels persist at the site. In 1999, when macrophytes were sampled twice, once in June and again in August, there was a marked seasonality of macrophyte cover. High plant cover in June (PVI=42%), was followed by a mid-summer 'crash' leading to a complete absence of plants by August. This phenomenon was observed in a number of sites in the 'training set' (Sayer & Davidson unpublished data).

The lake contains rudd, tench and pike. There were extremely high densities of small rudd and tench recorded in 1999 (Appendix 5).

5.3 Methods

5.3.1 Field methods

A core was retrieved from a central lake position in Kenfig Pool at 2.5 m water depth in July 2002 using a wide diameter (7.5 cm internal diameter) Livingstone type piston corer (Livingstone 1955). The core was 78 cm in length and was coded KENF2.

Two cores from Felbrigg Lake were used in the analysis presented here. FELB1 was collected in March 1998 using mini-Mackereth corer (internal diameter 5.2 cm) (Mackereth 1969) from the central area of the lake. FELB4 was retrieved in July 2000 from a slightly different area of the lake in the open-water zone using a Livingstone-type piston corer.

5.3.2 Lithostratigraphy

The percentage dry weight (%dw) for each sample was calculated by weighing approximately 1g of wet sediment in a pre-weighed crucible, from each pre-homogenised sediment layer, drying the sediment at 105 °C for at least 16 hours, then reweighing the crucible. Approximate organic matter content was then determined (as a percentage loss on ignition %LOI) by placing the crucible containing the dried sediment in a muffle furnace at 550 °C for two hours and then reweighing. The %carbonate content was calculated by returning the crucible to the furnace for two hours at 925 °C and then reweighing.

5.3.3 Radiometric analysis

Sediment samples from cores KENF2 and FELB1 were analysed for ^{210}Pb, ^{226}Ra, and ^{137}Cs by direct gamma assay in the Liverpool University Environmental Radioactivity Laboratory, using Ortec HPGe GWL series well-type coaxial low background intrinsic germanium detectors (Appleby et al. 1986). ^{210}Pb was determined via its gamma emissions at 46.5keV, and ^{226}Ra by the 295keV and 352keV γ-rays emitted by its daughter isotope ^{214}Pb following three weeks storage in sealed containers to allow radioactive equilibration. ^{137}Cs was measured by its emissions at 662keV. The absolute efficiencies of the detectors were determined using calibrated sources and sediment samples of known activity. Corrections were made for the effect of self-absorption of low energy γ-rays within the sample (Appleby et al. 1992).

FELB4 and FELB1 were correlated by means of their %LOI and %carbonate profile which displayed very similar patterns. The values for %LOI and %carbonate were so similar that given, the sampling intervals, the depths were considered equivalent between the cores.

5.3.4 Cladoceran analysis

Sub-fossil cladoceran samples were prepared and enumerated as outlined in Chapter 3. Fifteen evenly spaced samples in KENF2 were analysed. There was insufficient material remaining towards the top of the dated FELB1 core. Therefore, the eight lower samples came from FELB1 and the top two samples, (6–7 and 0–1 cm) came from FELB4. Thus, a total of ten samples were analysed from FELB1 and FELB4.

5.3.5 Macrofossil analysis

Profiles for plant macro-remains were generated in slightly different ways for each site. Fifteen levels of KENF2 were examined for macrofossils. The surface sediment sample had insufficient material so the adjacent sample (1-2 cm) was analysed. Sub-samples of approximately 20 cm^3 were washed through a 200 μm sieve, the exact sample volume being measured by water displacement (Birks 2001), and weighed. The entire residue on the 200 μm sieve was examined under a stereo-microscope at magnifications of X10-40 and all plant macro-remains were enumerated.

Data from a previous study of FELB1 are presented here (Burgess 1998). Sediment samples of between 30 cm^3 and 50 cm^3, the exact volume measured by water displacement, were sieved at 125 μm. The entire residue was then analysed under a binocular microscope at X10-40 magnification. Recognisable remains were isolated, identified and enumerated by comparison with modern reference material.

5.3.6 Numerical methods

The methods employed in reconstructions presented here are outlined in Chapter 3. A multivariate regression tree (MRT) was employed to model cladoceran assemblage response to zooplanktivorous fish (ZF) density and macrophyte percentage volume infestation (PVI) in August (APVI). The model produced six groups, representing distinct ranges of ZF density and APVI abundance, reflecting significant changes in ecological structure and function in shallow lakes. Redundancy analysis (RDA) was used to track graphically the temporal changes in ZF density and APVI. RDA was carried out on the surface sediment assemblages from the training set, constrained by ZF and APVI. The sedimentary assemblages were then passively placed in this analysis and their position within the bi-plot allowed the sample to be assigned to one of the MRT groups. A range of absolute values for APVI and ZF density could then be ascribed. Thus, position of the sample within the biplot reveals to which MRT group the sample belongs and the change in sample position provides a time-track of within-site variation in ecological space. Ordination analysis was carried out using CANOCO version 4.5 (ter Braak & Šmilauer 2002) on square-root transformed relative abundance data. Environmental data were either log, log (x+1) or square-root transformed dependent on which transformation best approximated a normal distribution of the data.

5.3.7 Historical records

For Felbrigg Lake various sources of historical evidence on past biological conditions were available. These were chiefly compiled in a Master's thesis (Burgess 1998). Kenfig Pool had records of fish stocking events kept by the local angling society and compiled by Giles (2002). In addition information on plant communities was available from a relatively recent survey (ENSIS 1996).

5.4 Results

5.4.1 Lithostratigraphy

5.4.1.1 Kenfig Pool

There were marked changes in the %LOI values throughout KENF2. The base of the sequence had very high organic content (>80%) which then declined to c. 20% at 45 cm with a subsequent steady rise to the top of the core (Fig. 5-1). The %carbonate content displayed a steady increase from around 2% at the base to the top of the core to 10% at the top.

5.4.1.2 Felbrigg Lake

There was very little variation in the dry weight and %LOI along the length of the core FELB1 and FELB4. Percentage carbonate content displayed a similar pattern between the two cores, increasing gradually from around 15% at 55 cm to a peak of around 30% at 35 cm and then declining steadily to around 20% at the surface of both cores (Fig. 5-2).

Figure 5-1. Summary lithostratigraphy for KENF2

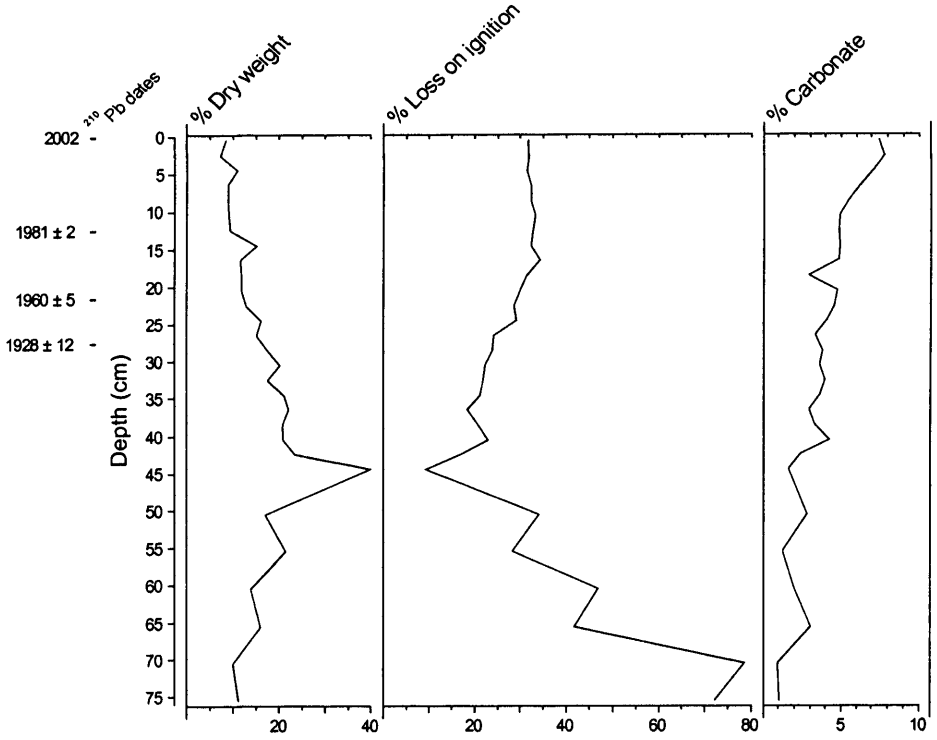
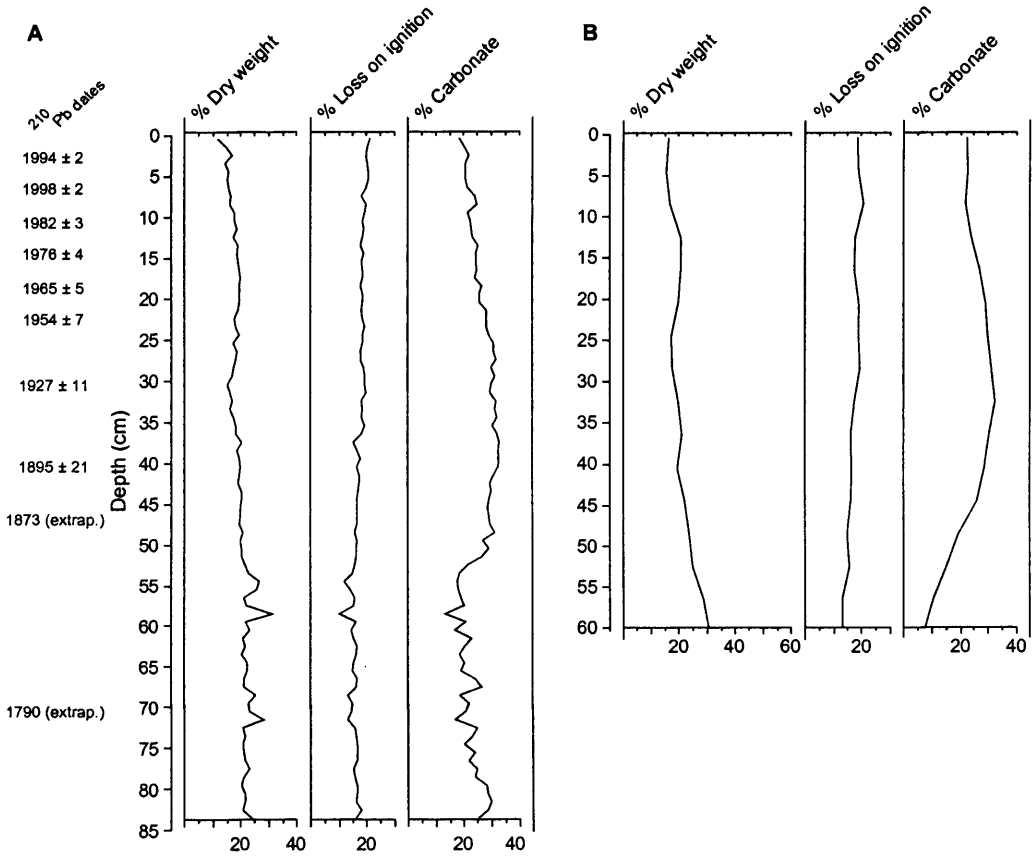


Figure 5-2. Summary lithostratigraphy for A) FELB1 and B) FELB4.



5.4.2 Radiometric analyses

5.4.2.1 Kenfig Pool

5.4.2.1.1 Lead-210 Activity

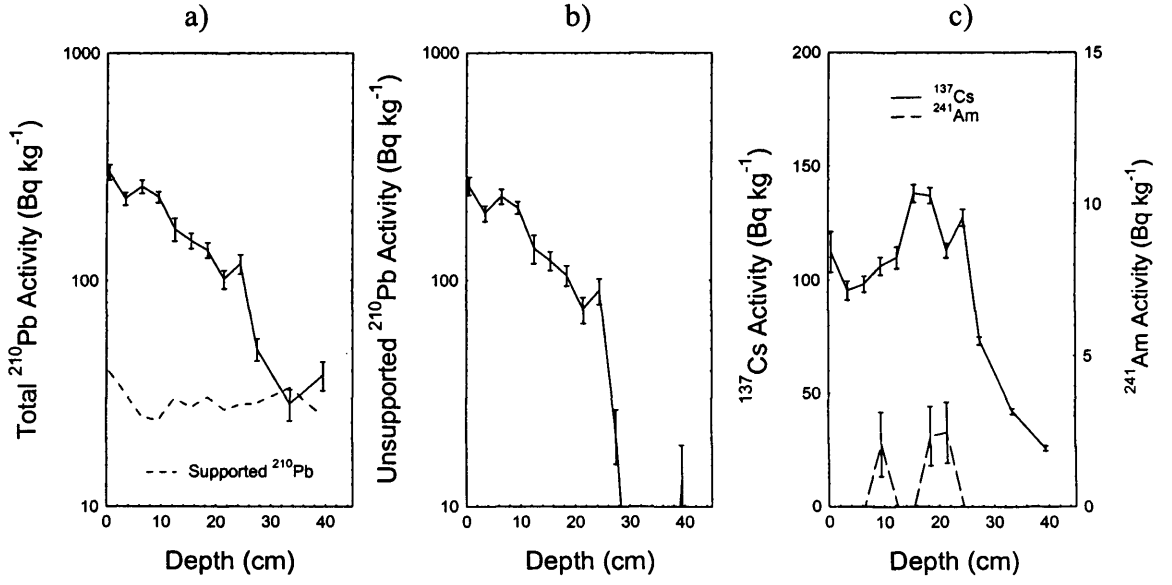
Total ^{210}Pb activity appears to reach equilibrium with the supporting ^{226}Ra at a depth of around 30 cm (Fig. 5-3a). Unsupported ^{210}Pb activity, calculated by subtracting ^{226}Ra activity from total ^{210}Pb activity, declines more or less exponentially with depth from the surface of the core down to about 24.5 cm (Fig. 5-3b). The much steeper decline below this depth could be an indication of a dilution event, or of a hiatus in the sediment record. The ^{210}Pb inventory of 4630 ±190 Bq m^{-2} corresponds to a mean ^{210}Pb supply rate of 144 ± 6 Bq m^{-2} y^{-1}. Since this is comparable to the estimated atmospheric flux (and to the value obtained for an earlier 1995 core from this site), if there is a hiatus in the sediment record it is unlikely to have occurred during the past few decades.

5.4.2.1.2 Artificial Fallout Radionuclides

The ^{137}Cs activity ve

rsus depth profile has a relatively poorly resolved peak between 15-25 cm that almost certainly records the 1963 fallout maximum from the atmospheric testing of nuclear weapons (Fig. 5-3c). This interpretation is supported by the presence of traces of ^{241}Am between 19-22 cm.

Figure 5-3. Fallout radionuclides for core KENF2 showing (a) total and supported ^{210}Pb, (b) unsupported ^{210}Pb, (c) ^{137}Cs and ^{241}Am concentrations versus depth.



5.4.2.1.3 Core Chronology

Figure 5-4 shows ^{210}Pb dates calculated using the constant rate of supply (CRS) and the constant initial concentration (CIC) dating models (Appleby et al., 1978), together with the 1963 depth suggested by the ^{137}Cs/^{241}Am record. The CRS model dates place 1963 at a depth of about 17.5 cm, a little above the depth suggested by the ^{137}Cs record. The CIC model dates are a little more irregular but suggest a 1963 depth of about 23.5 cm. The intermediate value of 20.5 cm is consistent with the ^{241}Am record and may provide the best estimate. Revised ^{210}Pb dates have been calculated using this as a reference point. The results, given in detail in Table 5-1, suggest a brief episode of rapid sedimentation ca. 1918. Dates and sedimentation rates during the early part of the 20th century are, however, a little speculative and should be regarded with some caution without supporting evidence. Excluding the episode of rapid accumulation, the mean sedimentation rate during the past 70 years is estimated to be 0.046 ± 0.007 g cm^{-2} y^{-1} (0.37 cm y^{-1}). During the past few decades there appears to have been a small but significant acceleration, with a mean sedimentation rate during the past 40 years of 0.057 g cm^{-2} y^{-1} (0.51 cm y^{-1}).

Figure 5-4. Radiometric chronology for core KENF2 showing the CRS and CIC model ^{210}Pb dates and the 1963 depth determined from the ^{137}Cs/^{241}Am record. Also shown are the revised ^{210}Pb dates and sedimentation rates calculated using the 1963 date as a reference point.

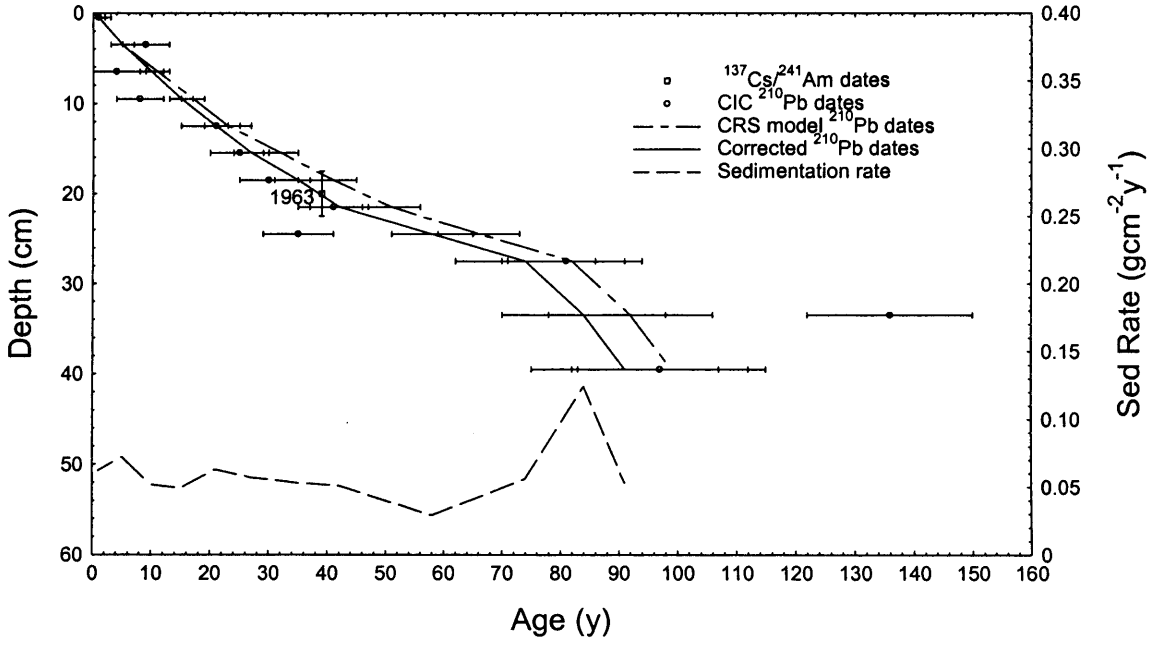


Table 5-1. Revised ^{210}Pb chronology of Kenfig Pool core KENF2

Depth		Chronology			Sedimentation Rate		
		Date	Age				
cm	g cm^{-2}	AD	Y	±	g cm^{-2} y^{-1}	cm y^{-1}	± (%)
0.0	0.00	2002	0	0			
0.5	0.04	2001	1	1	0.062	0.70	10.9
3.5	0.31	1997	5	2	0.072	0.67	10.3
6.5	0.62	1992	10	2	0.052	0.60	10.7
9.5	0.90	1987	15	2	0.049	0.55	11.0
12.5	1.19	1981	21	2	0.063	0.50	17.6
15.5	1.61	1975	27	3	0.057	0.43	15.6
18.5	2.00	1967	35	4	0.053	0.40	18.5
21.5	2.39	1960	42	5	0.051	0.26	23.2
24.5	2.85	1944	58	7	0.029	0.19	29.1
27.5	3.38	1928	74	12	0.056	0.35	44.6
33.5	4.64	1918	84	14	0.124	0.67	70.6
36.5	5.36	1915	88	15	0.088	0.35	68.3
39.5	6.08	1911	91	16	0.053	0.22	65.9

5.4.2.2 Felbrigg Lake

5.4.2.2.1 Lead-210 Activity

Equilibrium of total ^{210}Pb activity with the supporting ^{226}Ra, corresponding to c.150 years accumulation, was reached at a depth of about 43 cm (Fig. 5-5a). From the unsupported ^{210}Pb activity versus depth profile (Fig. 5-5b), two distinct zones can be distinguished. In the older part of the record (below 21-22 cm) concentrations decline more or less exponentially with depth, indicating relatively uniform sedimentation. Above 21-22 cm the profile has a distinct change in gradient, suggesting a recent increase in rates of sedimentation.

5.4.2.2.2 Artificial Fallout Radionuclides

The ^{137}Cs activity versus depth profiles (Fig. 5-5c) shows a sub-surface peak at about 14.5 cm recording the 1963 fallout maximum from the atmospheric testing of nuclear weapons. Because of the limited number of samples analysed it was not possible to locate the 1963 depth precisely, though it is reasonable to suppose that sediments from c. 14-20 cm date from the mid 1960s.

Figure 5-5. Fallout radionuclides for core FELB1 showing (a) total and supported ^{210}Pb, (b) unsupported ^{210}Pb, (c) ^{137}Cs and ^{241}Am concentrations versus depth.

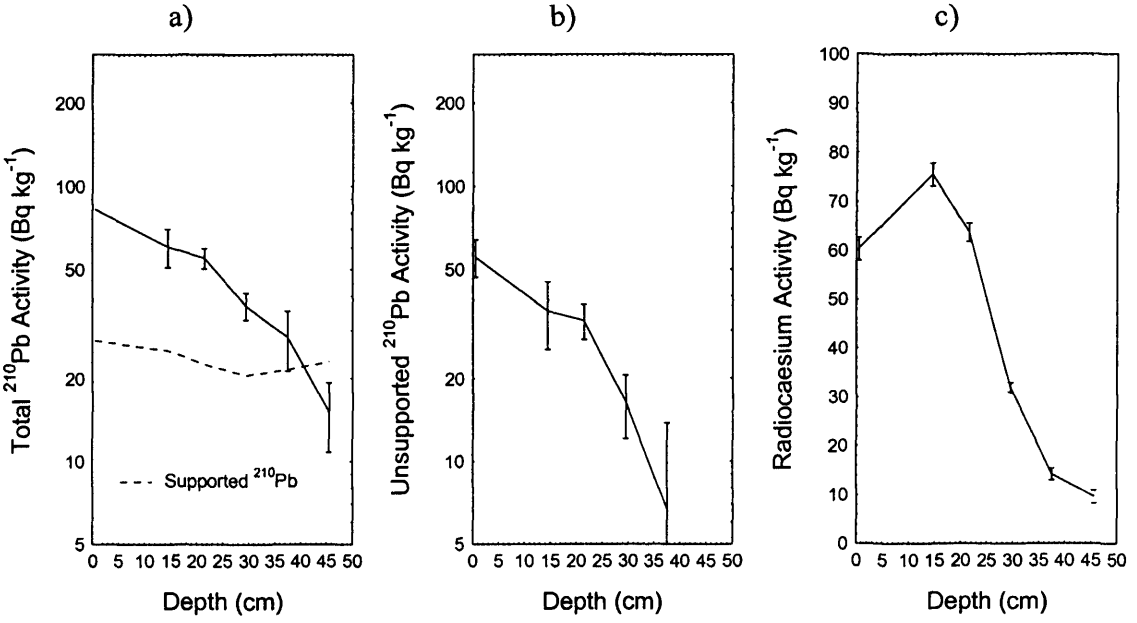
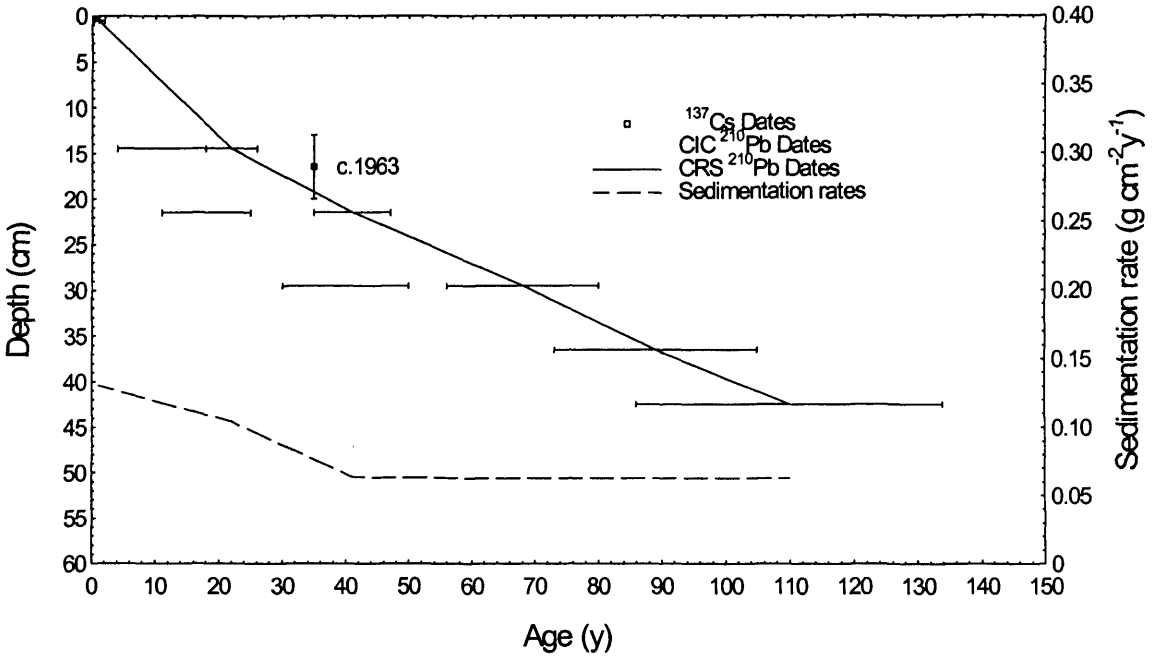


Figure 5-6. Radiometric chronology for core FELB1, showing CRS and CIC model ^{210}Pb dates together with 1963 depth determined from the ^{137}Cs stratigraphy. Also shown are sedimentation rates calculated using CRS model.



5.4.2.2.3 Core Chronologies

^{210}Pb chronologies were calculated using the CRS and CIC dating models (Appleby et al. 1978). Fig. 5-6 shows the results of the ^{210}Pb calculations, together with the approximate 1963 level suggested by the ^{137}Cs record. The CRS model indicates relatively uniform sedimentation rates of c. 0.062 g cm^{-2} y^{-1} up to the mid 1950s, after which they doubled, to a present day value of c. 0.13 g cm^{-2} y^{-1}. The CIC model gives a similar result for the period up to 1950, but suggests that the recent acceleration was later and more dramatic, occurring only during the past 20 years or so. The ^{137}Cs results suggest that the CRS model dates are more appropriate to this core, and these form the basis of the detailed chronology given in Table 5-2.

Table 5-2. Revised CRS model ^{210}Pb chronology for core FELB1

Depth		Chronology			Sedimentation Rate		
cm	g cm^{-2}	Date AD	Age Y	±	g cm^{-2} y^{-1}	cm y^{-1}	± (%)
0.0	0.00	1998	0				
0.5	0.07	1997	1	2	0.13	0.72	19.2
2.5	0.43	1994	4	2	0.13	0.69	20.8
4.5	0.80	1991	7	2	0.12	0.67	22.4
6.5	1.17	1988	10	2	0.12	0.64	23.9
8.5	1.54	1985	13	3	0.12	0.61	25.5
10.5	1.90	1982	16	3	0.11	0.59	27.1
12.5	2.27	1979	19	3	0.11	0.56	28.7
14.5	2.64	1976	22	4	0.10	0.54	30.3
16.5	3.07	1970	28	4	0.093	0.47	28.4
18.5	3.51	1965	33	5	0.081	0.40	26.6
20.5	3.94	1960	38	6	0.069	0.34	24.8
22.5	4.36	1954	44	7	0.062	0.30	24.2
24.5	4.77	1947	51	9	0.062	0.29	24.8
26.5	5.18	1940	58	10	0.062	0.29	25.4
28.5	5.59	1933	65	11	0.062	0.30	26.0
30.5	5.97	1927	71	11	0.062	0.34	
32.5	6.33	1921	77	12	0.062	0.34	
34.5	6.70	1915	83	14	0.062	0.33	
36.5	7.10	1909	89	16	0.062	0.30	
38.5	7.53	1902	96	18	0.062	0.29	
40.5	7.96	1895	103	21	0.062	0.29	

5.4.3 Cladoceran stratigraphies

5.4.3.1 Kenfig Pool

A total of 25 species of Cladocera was recorded from chitinous remains and 5 species or aggregate groups by ephippia. Complete cladocera counts are given in Appendix 6. Preservation appeared to be good with cladocera concentrations remaining relatively constant down core, with the exception of the 65 cm and 75 cm samples where concentrations were an order of magnitude lower than all other samples. Productivity may have been considerably lower at the base of the core. The cladoceran stratigraphy had three main sections.

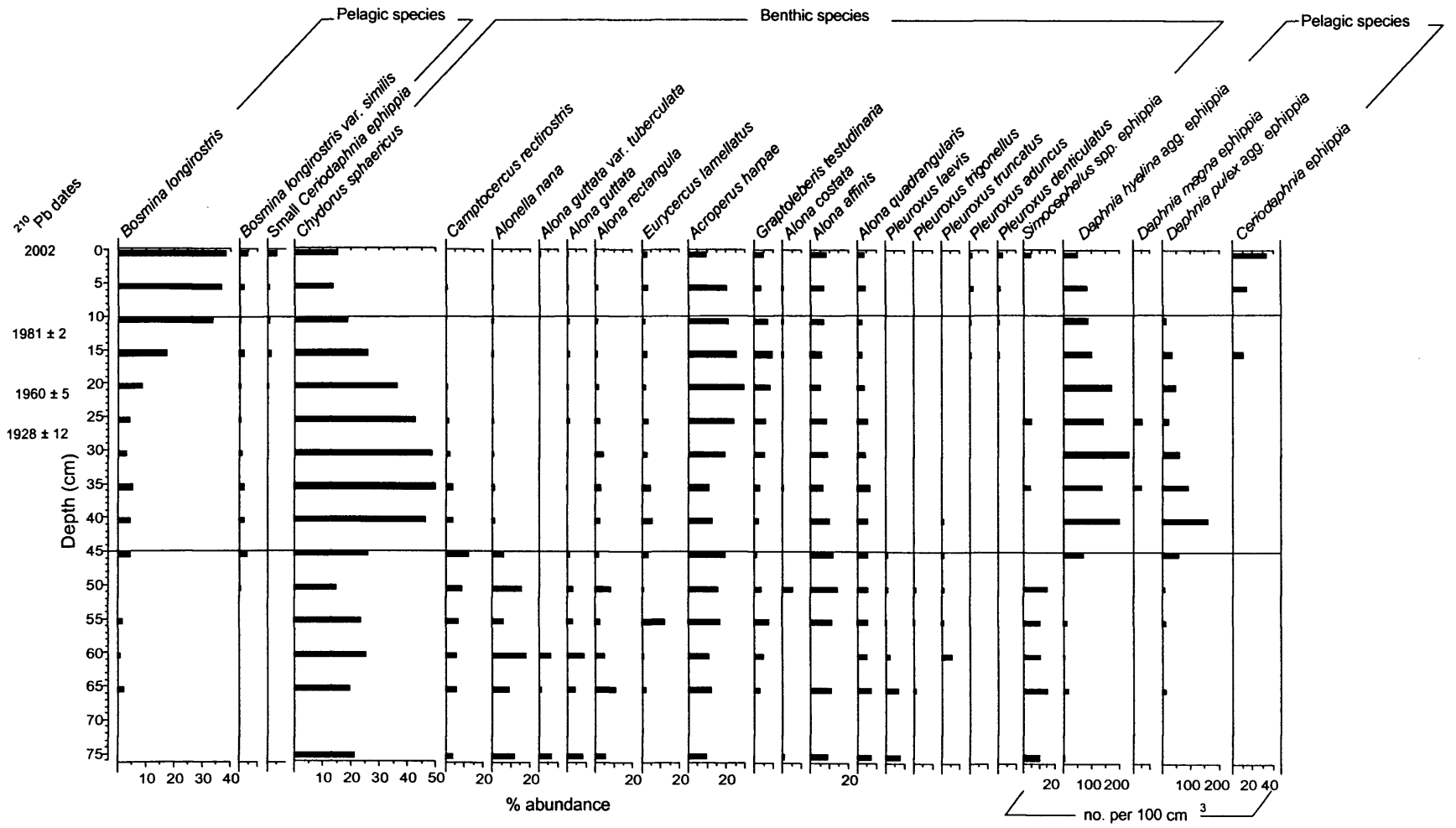
The bottom section of the core from 75-45 cm was characterised by relatively low numbers of *D. hyalina* agg. and *D. pulex* agg. ephippia and relatively high numbers of *Simocephalus* spp. ephippia (Fig. 5-7). The chitinous remains included strongly macrophyte-associated species, such as *P. laevis, A. harpae* and *Camptocercus rectirostris* Schölder (Hann 1989, Chapter 2) with a very low relative abundance of the small bodied pelagic *B. longirostris*. There were also several species present which tend to be mud-associated such as *Alona guttata* Sars, *Alona rectangula* Sars and *A. nana* (Hann 1989). There were subtle changes in the cladoceran assemblage throughout this section, probably corresponding to a period of several hundred years. There was a slight increase in *B. longirostris*, a decline in *P. laevis* with a concomitant shift to *P. truncatus*. There was also a small rise in the relative abundance of plant associated species; *E. lamellatus, A. harpae* and *G. testudinaria*. In contrast *C. sphaericus* abundance remained relatively constant.

In the transition between the lower section of the core and the middle section, between 45-11 cm there was a sharp rise in the abundance of the three types of *Daphnia* ephippia (Fig 5-7). *D. pulex* abundance peaked at 40 cm and then fell gradually to 10 cm. *D. magna* ephippia were present in low numbers in the 35 and 25 cm samples. *D. hyalina* ephippia numbers peaked between 40 cm and 20 cm at >200 ephippia per 100 cm^3. The start of the decline in *D. hyalina* ephippial abundance corresponded to around 1960. Concomitant with the fall in the numbers of the larger *Daphnia* spp ephippia was a rise in the *Ceriodaphnia* spp. numbers. There was a sharp rise in the abundance of *C. sphaericus* at 40 cm. *B. longirostris* increased steadily from around 20 cm (approximately 1960), coincident with a decline in *C. sphaericus* from the peak of 50% at 35 cm. With the exception of *A. harpae*

and *G. testudinaria*, there was a reduction in the proportion of benthic species such as *A. nana* and *A. rectangula*. The large increases in *Daphnia* spp. ephippia at around 40 cm probably correspond to the late 19th to early 20th century. This period in the lake's history appears to have seen a shift to planktonic (*Daphnia*) and semi-planktonic (*C. sphaericus*) species.

The top of the core (11-0 cm) was characterised by the increased dominance of *B. longirostris*, a small planktonic cladoceran and an increase in the proportion of *B. longirostris* var. *similis*. The relative abundance of *C. sphaericus* fell and there was a switch in the *Pleuroxus* species to *P. aduncus* and *Pleuroxus denticulatus* Birge. The proportions of species, such as *A. harpae, G. testudinaria, E. lamellatus, Alona affinis* Leydig and *Alona quadrangularis* Sars were relatively constant.

Figure 5-7. Summary cladoceran stratigraphy for KENF 2, ephippial remains are on the right hand side of the diagram.



5.4.3.2 Felbrigg Lake

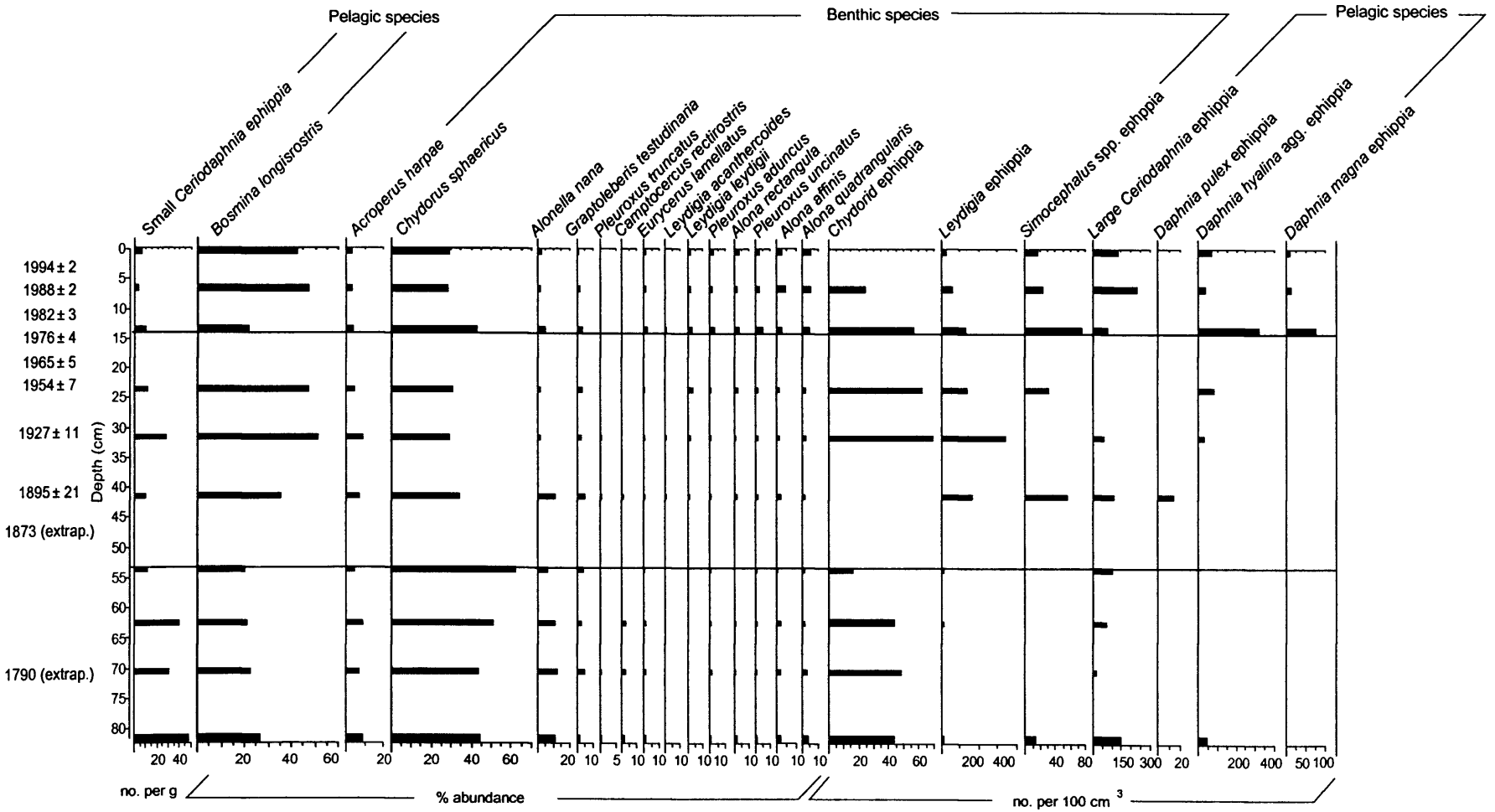
A total of 26 cladoceran species or species aggregates were recorded by chitinous and ephippial remains (Appendix 6). Preservation appeared to be good with little variation in concentration of remains, although there was a slight decrease in the concentration of sub-fossils towards the top of the core, correlating with decreasing sediment density. There were again three main sections discernible in the cladoceran stratigraphy.

From the core bottom to 54 cm the assemblage was relatively stable (Fig. 5-8), dominated by *C. sphaericus* with a relatively low abundance of *B. longirostris*. There was, in addition, a diverse array of benthic species including *G. testudinaria, P. truncatus* and *C. rectirostris*. The dominant ephippial remains were of *Ceriodaphnia*, *Daphnia*, was present in only one sample in this period.

At 54 cm there was a shift in community composition as *C. sphaericus* declined and *B. longirostris* increased. The abundance of *A. nana* and *P. truncatus* fell and *C. rectirostris* disappeared from the record. The chitinous remains of both *Leydigia leydigii* Schödler and *Leydigia acanthercoides* Fischer and their ephippia appeared in the record. *Daphnia* ephippia were consistently present in this period of the record, first as *D. pulex* agg. and then as *D. hyalina* agg., albeit in relatively low numbers.

There were step changes in the assemblage composition between the samples at 23-24 cm and 13-14 cm. The relative abundance of *B. longirostris* fell sharply and *C. sphaericus* increased. Numbers of the large bodied, plant-inhabiting *Simocephalus* spp. ephippia increased sharply as did the abundance of *Daphnia* ephippia, with the large bodied *D. magna* appearing in the record for the first time. The top two samples were similar exhibiting a shift from *Daphnia* spp. to *Ceriodaphnia* spp. and a return to numerical dominance of *B. longirostris* over *C. sphaericus*. In addition there were subtle changes in some of the other species with *A. quadrangularis, A. affinis* and *A. rectangula* all becoming more abundant towards the top of the sequence. *A. harpae* displayed a relatively smooth reduction in its relative abundance along the length of the core.

Figure 5-8. Summary cladoceran stratigraphy from Felbrigg lake, the bottom eight samples were from FELB1 and the top two from FELB4.



5.4.4 Inference model results

5.4.4.1 Kenfig Pool

The was a stable assemblage at the base of KENF2, with the model predicting membership of group C which equates to a zooplanktivorous fish density below 0.51 fish m^{-2} and clear water and abundant macrophyte coverage (Fig. 5-9). The movement in ordination space between the samples of 50-51 cm and 45-46 cm reflects a step change in the sub-fossil cladoceran assemblage. There was no shift, however, in the MRT group, as the overall ecological functioning remained the same. The model continued to predict clear water, abundant macrophytes and low fish predation pressure. The direction of movement between the samples may indicate a reduction in macrophyte PVI associated with the deepening of the lake and the shift from wetland to more open water conditions. Between 45 and 20 cm there was a period of stability followed by a steady shift in ordination space, above 20 cm, indicative of an increase in ZF predation pressure. There was a change in MRT group from C to D, at 5-6 cm and then to group B for the surface sample. These changes suggest a steady increase to >0.51 fish m^{-2} for group D and then >0.655 fish m^{-2} for group B.

5.4.4.2 Felbrigg Lake

The base of FELB4 indicates stability of ecological structure and function from 82 cm to 41 cm (Fig. 5-10). The origin of the lake as a 'stew pond' for fish production may be the cause of the relatively high fish predation indicated by the model for this period. Group B has high macrophyte cover (>10.3% PVI) and high ZF abundance (>0.655 fish m^{-2}). There was a relatively large shift in the sub-fossil assemblage between 41 cm and 31 cm. However, the MRT group membership remained the same. From 31 cm to 13 cm there was a MRT group changed from B to D and subsequently to C indicating a reduction in the ZF density. Thereafter, a sharp increase in ZF density was indicated by the model. The surface sediment from the core along (FELB4) along with the passively placed surface sediment from the training set analysis (Chapter 4), both indicate that the lake is currently placed in MRT group A. Group A has very low APVI and high ZF density. Lakes in group A are generally turbid, phytoplankton dominated systems where phytoplankton production dominates and macrophytes are absent by August. This accords well with recent observations at Felbrigg Lake.

Figure 5-9. Time track of the sedimentary assemblages of KENF2 (Kx-x+1 (cm), ✖) passively placed in the RDA biplot constructed from the surface sediment assemblages from the training set sites (Chapter 4) bounded by the critical values for APVI and ZF of the MRT groups.

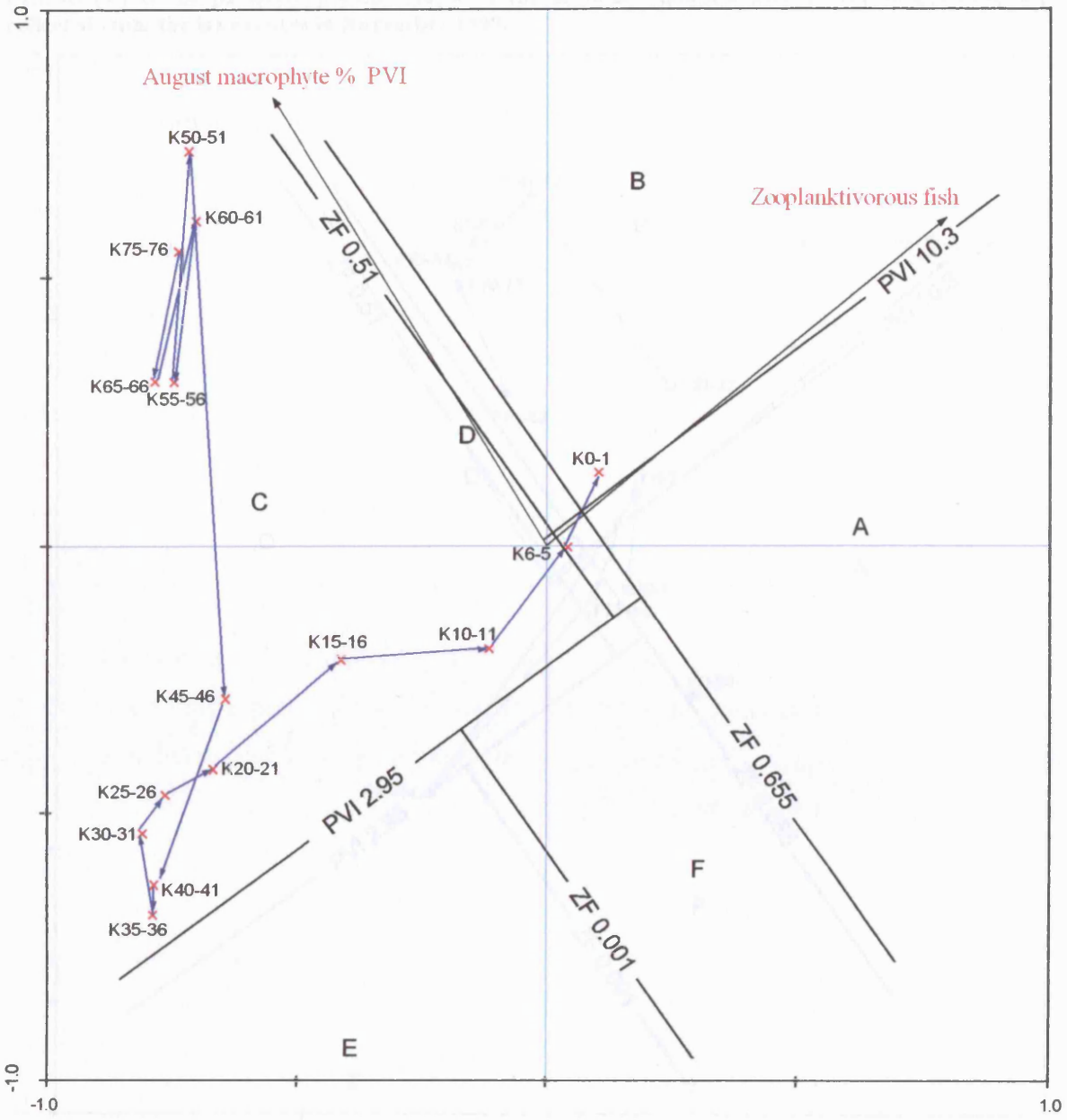
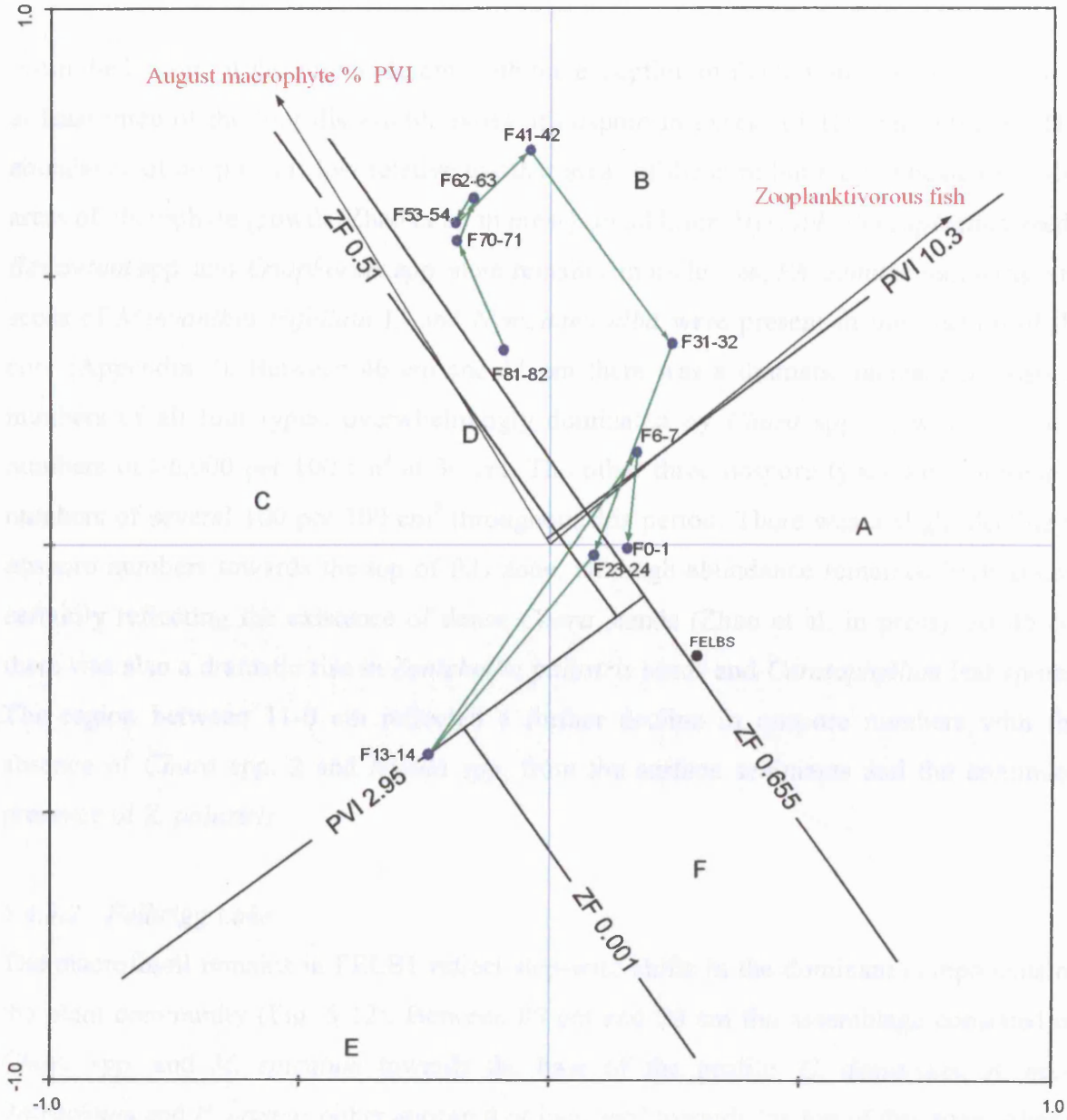


Figure 5-10. Time track of the sedimentary assemblages of FELB1 and FELB4 (Fx-x+1 (cm), ●) passively placed in the RDA biplot constructed from the surface sediment assemblages from the training set sites (Chapter 4) bounded by the critical values of APVI and ZF of the MRT groups. FELBS (●) is the passively placed sample of the sediment samples used in the model calibration collected from the lake centre in November 1999.



5.4.5 *Macrofossil stratigraphy*

5.4.5.1 *Kenfig Pool*

The macrofossil sequence at Kenfig Pool was dominated by the remains of charophytes. It was possible to identify four morphologically distinct types of oospore, one of *Nitella* and three of *Chara*. Unfortunately, it was not possible to identify the oospores to species-level. The concentration of oospores present in this core was exceptionally high (around 7,000 per 100 cm^3) when compared to other studies (Odgaard & Rasmussen 2001, Davidson et al.

2002, Zhao et al. 2005). *Chara* oospores showed large changes in abundance from complete absence in the lowest sample analysed to >7,000 per 100 cm^3 at 36 cm (Fig. 5-11).

From the bottom of the core to 46 cm, with the exception of the bottom sample, there were at least three of the four discernible types of oospore in excess of 100 per 100 cm^3. This abundance of oospores is low relative to other areas of the core but may indicate extensive areas of charophyte growth (Zhao et al. in press). In addition *Myriophyllum spicatum* seeds, *Equisetum* spp. and *Eriophorum* spp. stem remains, moss leaves, *Phragmites* root parts, and seeds of *Menyanthes trifoliata* L. and *Nymphaea alba* were present in this section of the core (Appendix 7). Between 46 cm and 11 cm there was a dramatic increase in oospore numbers of all four types, overwhelmingly dominated by *Chara* spp. 1, which reached numbers of >6,000 per 100 cm^3 at 36 cm. The other three oospore types were present in numbers of several 100 per 100 cm^3 throughout this period. There was a slight decline in oospore numbers towards the top of this zone, although abundance remained high almost certainly reflecting the existence of dense *Chara* stands (Zhao et al. in press). At 45 cm there was also a dramatic rise in *Zanichellia palustris* seeds and *Ceratophyllum* leaf spines. The region between 11-0 cm reflected a further decline in oospore numbers with the absence of *Chara* spp. 2 and *Nitella* spp. from the surface sediments and the continued presence of *Z. palustris*.

5.4.5.2 Felbrigg Lake

The macrofossil remains in FELB1 reflect step-wise shifts in the dominant components of the plant community (Fig. 5-12). Between 85 cm and 50 cm the assemblage consisted of *Chara* spp. and *M. spicatum* towards the base of the profile. *C. demersum*, *R.* sect. *Batrachium* and *P. crispus* either appeared or increased towards the top of this zone. Above 45 cm *M. spicatum* disappeared and the numbers of *Chara* spp. oospores declined. Concomitant with the loss of *M. spicatum*, remains of *C. demersum*, *R.* sect. *Batrachium* and *P. crispus* increased in abundance and *Z. palustris* remains appeared, albeit in very low numbers. At a depth of around 20 cm there was a further change in the macrofossil assemblage to dominance by *Z. palustris* with a low incidence of *C. demersum* and *R.* sect. *Batrachium*. One feature of note in the profile was the apparent recovery of *Chara* spp. at around 10 cm, probably corresponding to the late 1970s or early 1980s.

Figure 5-11. Macrofossil stratigraphy for KENF2 only the dominant taxa are shown.

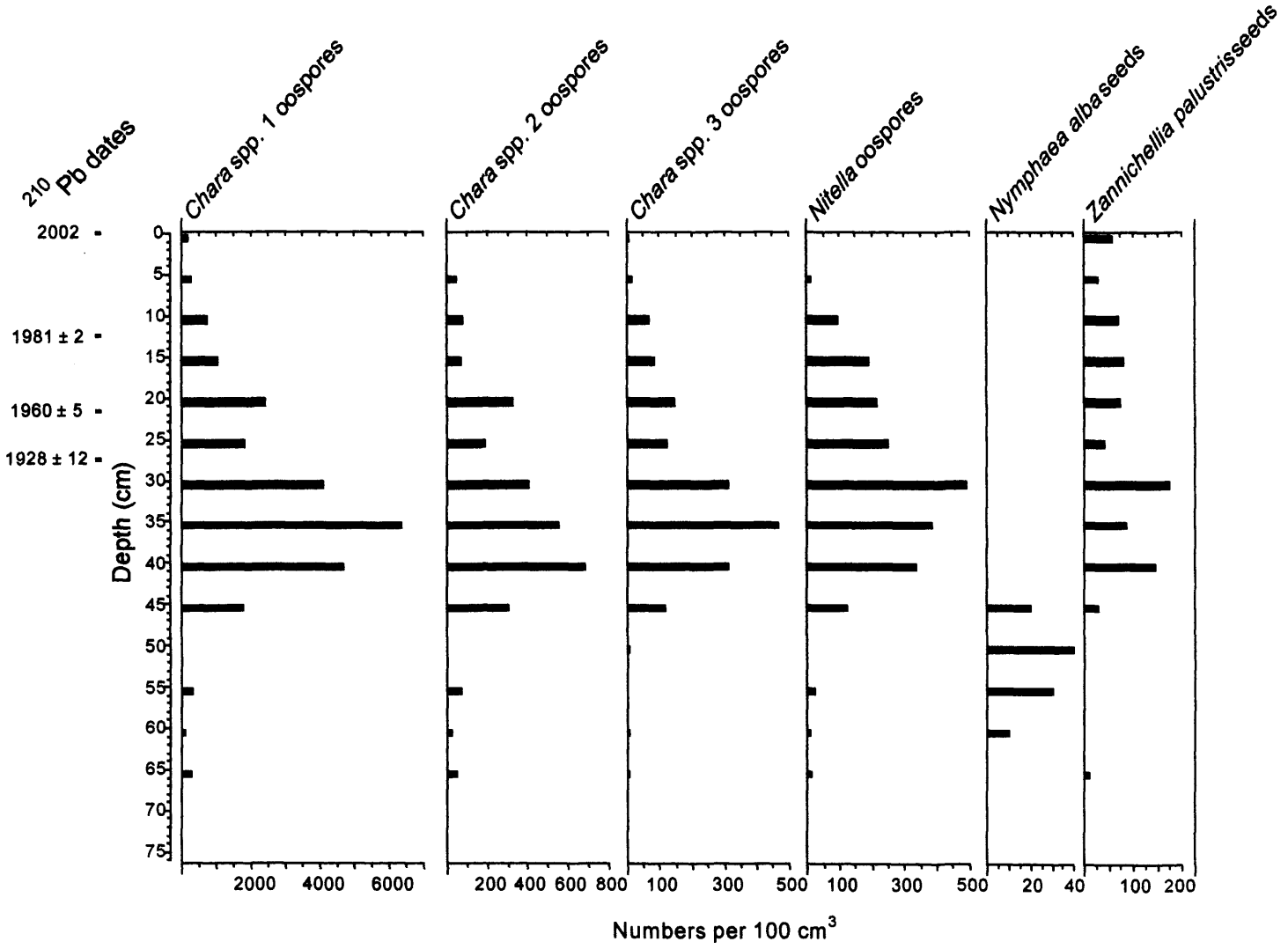
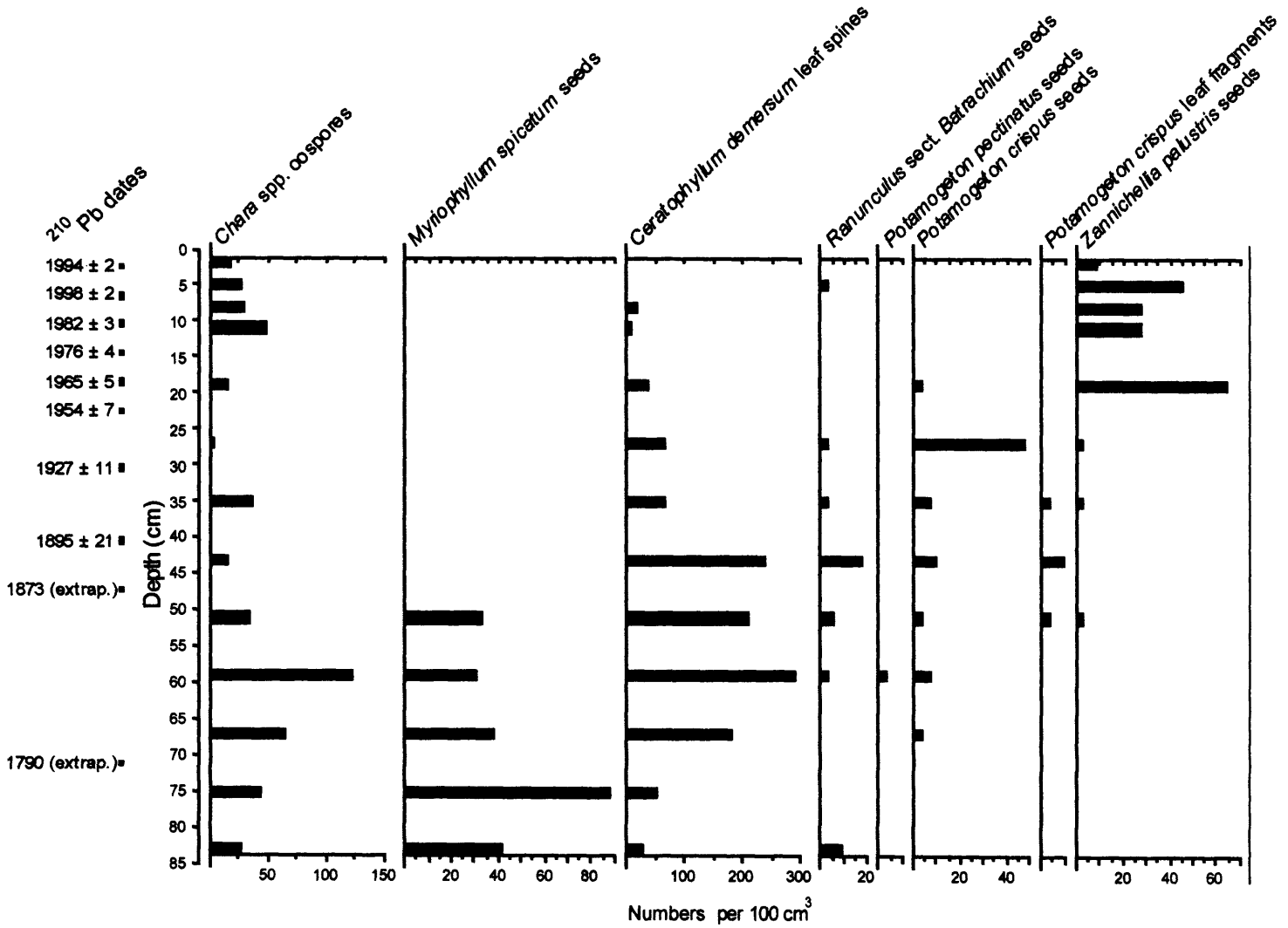


Figure 5-12. Summary macrofossil stratigraphy for FELB1, only submerged species are shown (data from Burgess 1998).



5.4.6 Historical records

Historical records on fish stocking for Kenfig Pool come from the local angling association and were compiled as part of a project conducted by Giles (2003). Prior to the documented records of fish stocking the lake was reported to contain perch, sticklebacks (*Gasterosteus aculeatus aculeatus* L.) and Eel (*Anguilla anguilla* L) (Giles 2003). The first documented record of stocking was for 'mixed coarse fish' in 1957 There has been a fairly continuous practice of stocking since 1957 (Table 5-3). During the 1960s stocking was exclusively rainbow (*Onchorhyncus mykiss* Walbaum) and brown trout (*Salmo trutta* L.). Subsequently perch and then carp were stocked in the 1980s and in the late 1980s and early 1990s tench and rudd were added to the list of species stocked in the lake. There is some anecdotal evidence for a changing fish community in recent years at Kenfig Pool. The site was previously known for the large tench and rudd it held, but there has been a decline in these 'specimen' fish. This may suggest a shift to a community dominated by smaller individuals.

Table 5-3. Known recent fish stocking at Kenfig Pool.

Species	Date	Number / Weight
Mixed coarse fish	1957	3,000
Rainbow trout	1962	250
Rainbow trout	1963	500
Brown trout	1964	250
Rainbow trout	1964	250
Brown trout (fry)	1968	500
Brown trout	1968	250
Brown trout	1973	200
Perch	1981	750
Perch	1982	550
Carp	1987	300 lb
Rainbow trout	1988	650
Brown trout	1989	300
Rainbow trout	1991	1,000
Tench	1992	2,000
Rudd	1993	2,000

There are a number of anecdotal records for changes in the fish community at Felbrigg Lake (Burgess 1998). Perch were historically present, but the population was reportedly lost to the viral perch disease prevalent in the 1970s. In addition, the lake was netted for

eels in the 1980s. The combination of the loss of perch and the reduction in eels may have removed the dominant piscivores and reduced the predation pressure on smaller fish. The tench population, in particular small individuals, was reported to rapidly increase at this time (Bailey 1984). Currently Felbrigg Lake is dominated by small rudd with a substantial tench population.

5.5 Discussion

5.5.1 Core chronologies

The chronology for KENF2 for the last century appears to be reliable, showing a small but significant rise in accumulation rates over the last 20 years. The increase in %LOI and decrease in %dry weight may indicate an increase of within-lake production.

The dramatic changes in the lithostratigraphic characteristics of the sediments over the time period represented by KENF2 means a uniform sedimentation rate cannot be assumed. The uncertainty in the data on the accumulation rate around the turn of the 19th century makes the precise estimation of the time period represented by the core problematic. Nonetheless, the core covers no less than 400 years.

The use of material from two different cores, FELB1 and FELB4, taken from slightly different areas of the lake introduced a degree of uncertainty to the chronology of the cladoceran sequence. There were, however, repeatable %LOI and carbonate profiles between FELB4 and FELB1. It is likely, therefore, that the two cores had very similar accumulation rates such that the radiometric chronology established for FELB1 can be reliably applied to samples from FELB4.

There is likely to be some spatial heterogeneity in the sedimentary cladoceran remains. Thus, the question remains as to whether the changes observed in the top two samples, from FELB4, result from sedimentary patchiness or changes of within-lake biological structure. The surface sediment sampled as part of the calibration exercise from the open water in November 1999, in the same location as FELB1, had a very similar composition to

FELB4 (Fig. 5-10, Appendix 6). This suggests that any spatial variation present does not preclude the use of the sediments from FELB4 to infer change and that the data (from FELB4) reflect genuine alterations in biological structure and function rather than spatial patchiness of remains.

5.5.2 Inferring past environments

When applied to the data the inferences of the model indicated that both sites have gone through dramatic and gradual changes in their ecological functioning on a timescale of decades to centuries.

5.5.2.1 Kenfig Pool

The MRT model indicates that Kenfig Pool has gone through two major periods of change in ecological function. The first was dramatic step change in the late 19th century (45 cm) and a second more gradual between around 1960 (20 cm) and the present. In spite of the large movement in ordination space associated with the initial change there was no change in MRT group. The model, therefore, did not explicitly indicate any change in APVI or ZF density. The sub-fossil cladoceran and macrofossil data, however, strongly indicate a shift in ecological state or functioning.

There were documented changes in water level at Kenfig Pool in the late 19th century. Thus, the lake may have been enlarged and deepened at this time. Deepening water and a shift to submerged aquatic plant community dominated by *Chara* spp from one consisting of more emergent plant species, such as *Equisetum* spp. *M. trifoliata* and *Eriophorum* spp. may reflect an increased area of open water and a deepening of the site. Higher water levels and newly flooded land may have resulted in the release of nutrients. This combined with fish community reportedly dominated by piscivores, eel and perch (Giles 2003) may have resulted in a relatively large pelagic area and low ZF density. This in turn this may have resulted in the observed increase in the proportion of large bodied pelagic species, such as *Daphnia,* and may explain the abundance in the community of the plant-associated but semi-planktonic species *C. sphaericus*. Thus, the large shift in cladoceran community structure in the late 19th century may have resulted from a shift from a system based almost

exclusively on benthic productivity to one where pelagic productivity became more important. In this case as a result of changing water levels rather than eutrophication.

From 1960 the model predicted a steady increase in ZF predation pressure with a shift from functional group C to A via D. Thus, the model indicates that the site has never been turbid, and has always contained abundant submerged vegetation, but that since the 1960s there has been a steady increase in ZF density. Comparison with fish stocking records suggests that the model has accurately reconstructed the timing and magnitude of the changes in ZF fish density. Kenfig Pool was known for its rudd and tench population in the 1970s and early 1980s (Giles 2003). Tench are largely insectivorous and rudd is a less voracious zooplanktivorous species than roach (Moss et al. 1996a), perhaps accounting for the gradual rather than dramatic change in the cladoceran assemblage. The steady increase in the inferred levels of zooplanktivory may indicate change in the structure of the fish community with increasing dominance of smaller individuals. This is in agreement with the reported decline in the 'specimen' fish for which the site was previously known (Giles 2002).

The surface sediment assemblage placed Kenfig Pool within group B indicating the site has relatively high APVI, at least greater than 10%, and a ZF density higher than 0.655 fish m^{-2}. The prediction of the plant abundance is accurate in that the site currently maintains an abundant plant community throughout the summer (EA unpublished data 2004). The prediction of fish abundance is less clear. A recent survey carried out in March 2003 (Giles 2003) found low numbers of rudd, tench and perch. Furthermore, fish sampling in 1977 and 1998 indicated a switch in dominance from rudd to perch in this period. However, numbers were consistently high. The sampling technique used, seine netting, does not tend to catch the very smallest individuals (Perrow et al. 1996). Thus, there may have been a shift to dominance by smaller individuals over the past few years. An alternative hypothesis is that reportedly high cormorant predation has depleted the population over the past years. Most fish caught in the 2003 survey bore scars from cormorant attack and Giles (2003) suggests that the lower fish abundance may be due to high cormorant predation pressure. Whilst reducing overall biomass this would also reduce competition and perhaps predation on the smallest individuals and may result in the prediction of relatively high ZF predation pressure. Given that the surface sediment sample is probably an amalgam of the past 3-5

years at this site, the model is likely to reflect the fish community sampled in 1998, which contained large numbers of both small perch and rudd and may well have corresponded to a density greater than 0.655 fish m^{-2}.

There was no reliable relationship between nutrient concentration and cladoceran assemblage (Chapter 4). There was, however, some association between the MRT delimited groups and other environmental variables. Sites in group A, characterised by high PVI and ZF were also associated with clear water and low nutrient (TP and nitrate) concentrations. This is consistent with measured values (<50 $\mu g\ l^{-1}$) for Kenfig Pool from recent years (EA unpublished data, 2004).

The macrofossil data indicate that the effects of repeated fish stocking may have cascaded down the trophic levels and have had a deleterious impact on the conservation value of the site. The sedimentary remains of plants suggest a decline in the abundance of *Chara* and *Nitella* from around the time that fish were introduced into the lake. The model does not, however, suggest any change in PVI or any further shift to a more planktonic system. This is in good agreement with modern data as the lake has abundant macrophytes throughout the growing season. The model, therefore, did not appear to be sensitive to the change in species composition of submerged macrophytes.

5.5.2.2 Felbrigg Lake

The inferred changes in ecology indicate that Felbrigg Lake has undergone substantive changes in ecological structure and function over the last 200 years. The base of the sequence suggests that fish predation pressure within the lake has always been fairly high. Between 82-41 cm there was a period of stability in ecological structure, with high inferred APVI and relatively high ZF predation pressure but with low Chla and clear water. Thus, it is likely that epilimnetic primary production was limited by nutrients and that the benthic production dominated. Between 42 cm and 31 cm the large movement in ordination space in the biplot suggested a relatively large shift in the lake's functioning, there was not, however, a shift in MRT group membership. Thus, there was no inferred change in APVI or ZF density. The macrofossil profile suggested a concomitant shift in the submerged flora of the site at this time, with a reduction in *Chara* spp., the loss of *M. spicatum* and the increased abundance *C. demersum*, a species more associated with higher nutrient

concentrations. These changes in submerged flora and the shift in cladoceran assemblage between 42 cm and 31 cm, corresponding to around 1850, may reflect a shift in the ecological functioning with an increase in the importance of planktonic production at Felbrigg, perhaps in response to eutrophication (Vadeboncoeur et al. 2003). Thus, whilst there may not have been a reduction in PVI, there may even have been an increase, it is likely there was a shift in ecological functioning resulting, perhaps from less nutrient limitation of pelagic primary production.

From 31 cm to the surface there were dramatic movements in ordination space between sample and between MRT delimited group chiefly associated with alterations of the fish community. The model inferred a decline in ZF density at 23 cm and then again at 13 cm. The former sample placed the site in group D and the latter sample fell on the cusp of groups C and E, suggesting a significant decline in zooplanktivory during this period. The lake has undergone a number of documented changes in fish community since the 1970s. The step changes in cladoceran assemblage between sample at 23-24 cm and 13-14 cm may result from the loss of perch. The perch population suffered from the prevalent viral disease in the 1970s and anecdotal evidence suggests there was a subsequent explosion of the tench population, with large numbers of small tench dominating the site (Bailey 1984). Whilst perch are piscivorous upon attaining a sufficient gape size, they are zooplanktivorous in the first stages of their life (Persson & Eklov 1995). Thus, their loss in combination with an increased tench population may have reduced the predation pressure and explain the observed changes in cladoceran assemblage. The effects of this reduction of zooplanktivory may have cascaded down the trophic levels (Pace et al. 1999), resulting in a greater abundance of large-bodied cladocerans and relatively clear water. The macrofossil stratigraphy may support this assertion as there was a slight rise in charophyte oospore numbers at this time, perhaps reflecting clearer water and improved conditions for Characeae.

The further modification of the cladoceran community post 1970s ($\approx$15 cm) indicates perhaps a slight increase in APVI but a very sharp increase in zooplanktivory to the sample at 5-6 cm. The inferred shifts accord well with the anecdotal records for the site and with recent sampling of the fish community. The reported netting of the eel population in the 1970s is likely to have reduced piscivory on ZF (Burgess 1998). The decline in piscivorous

species, perch and eels, appears to have resulted in a change in the balance of the fish population releasing rudd from predatory control and resulting in the high zooplanktivory indicated by the model. The cladoceran surface sediment assemblage places Felbrigg in group A, the characteristics of which are very low or absent APVI and high ZF density. This accorded well with the data for Felbrigg collected in 1999-2000. Macrophytes were present in early summer, but absent by August and the fish community was dominated by very high densities of small rudd and tench (Appendix 5).

5.5.3 Movement in ordination space within MRT group

The comparison of the cladoceran inferred values with historical data suggest that the movement of samples within the biplot may accurately reflect the change in past ZF predation pressure at both Kenfig Pool and Felbrigg Lake. Thus, even where there is no change in MRT group the data suggest that movement within ordination space along the axis corresponding to ZF density represents a falling or rise in ZF predation pressure. Whilst no absolute values can be ascribed to these within group changes the relative change in abundance appears to be genuine.

The within-MRT group shifts within the biplot along the axis represented by APVI may not, however, result from a simple increase or reduction in macrophyte PVI. The shift between the samples at 50-51 cm to 45-46 cm at Kenfig Pool may indicate an increase in the pelagic area, and perhaps productivity, that occurred with a change in water level, rather than any alteration in overall APVI. The change may have been from relatively swampy conditions with fluctuating water levels to a larger, more permanent, area of open water and dominance of *Chara* spp above 45 cm. The *Chara* spp. may have been a very low growing species and could have resulted in a decline in APVI. Alternatively, the model may be reflecting changes in the form of primary production over time. For example there was a large shift in ordination space early in records of the two sites, with no change in MRT group. The macrofossil data at both sites indicated some alteration in the dominant component of the submerged aquatic flora concomitant with this shift in cladoceran assemblage. The record is more difficult to interpret at Kenfig as it is complicated by the deepening of water and expansion of the area of the lake. At Felbrigg, however, the change in submerged flora, reflected by the macrofossil record, may have resulted from nutrient

enrichment (James et al. 2005). The direction of the movement of the cladoceran assemblage based time track in ordination space at that time is towards lower APVI. Whether there was a decline in APVI at Felbrigg at this time is, however, moot. There may well have been an increase APVI concomitant with the shift in community from *Chara* spp and *M. spicatum* to *C. demersum*. Thus, the direction of the time track within a MRT group on the axis corresponding to APVI may reflect a change in APVI between those samples. It may however reflect the shifting balance of planktonic and benthic forms of primary production that are associated with eutrophication (Liboriussen & Jeppesen 2003, Vadeboncoeur et al. 2003).

5.6 Conclusion

This study is the first application of a new palaeoecological technique capable of providing simultaneous, semi-quantitative estimates of past ZF density and aquatic macrophyte PVI from the month of August. Comparison of the inferred values with the plant macrofossil records and known changes in fish community provided a partial verification of the models veracity. The model predictions tally well with historical and supporting palaeolimnological data. This method, therefore, appears to reliably track eutrophication induced changes in the ecological structure and function in shallow lakes. The long-term perspective provided by the palaeolimnological record may elucidate the nature and causes of shifts in aquatic ecosystem functioning in response to perturbation.

6 Chapter 6 – Summary, conclusions and future directions

6.1 Introduction

The primary focus of the research contained in this thesis was to investigate the potential of sub-fossil cladoceran assemblages to infer eutrophication related changes in shallow lake ecosystem structure and function. The different sections (chapters) of this study represented a logical progression of analysis of zooplankton communities in shallow lakes across both spatial and temporal scales and the key findings are summarised below. The chapter concludes with an assessment of the applications for management and ideas for future research directions.

6.2 Summary

Section 1 - The study was founded on the axiom that an understanding of contemporary zooplankton ecology was vital for the development of a robust palaeoecological inference model. To this end a significant component of the project investigated contemporary zooplankton community structure. The first section of the thesis, therefore, set out to determine the forces shaping zooplankton community composition sampled from both the centre and the edge of 39 shallow lakes. Canonical correspondence analysis (CCA) indicated that zooplanktivorous fish density (ZF) and August macrophyte abundance, expressed as percentage volume infestation (APVI), were the most significant explanatory variables in the central lake community. At the lake edge secchi depth explained the most variation in the zooplankton community and ZF, whilst still statistically significant explained a smaller percentage of the variance. Logistic regression was then employed on species presence/absence data to investigate individual species response to the environmental gradients within the data set. A number of pelagic and benthic (sediment or plant associated) species displayed significant responses to multiple factors. For example, the presence of *D. hyalina/longispina* and total *Daphnia* in the centre of the lakes were best

predicted by a combination of ZF and APVI. For the pelagic taxa there was a shift from large bodied to small bodied taxa as ZF increased in the central lake samples. In the lake edge, however, large bodied species generally persisted at higher ZF density. Furthermore, in the lake edge there was a non-linear response of *D. hyalina/longispina* to ZF with the likelihood of occurrence increasing at high ZF abundance. The mechanism for the non-linear response was probably attributable to an indirect ecosystem feedback effect. One possible mechanism was the reduction in the efficacy of visual predators by a decrease in water clarity to a point at where larger bodied species could occur. The logistic regression also suggested some size selective predation of plant associated species.

Section 2 - If the principles established from the study of contemporary communities were to be translated to the sub-fossil communities it was vital that a coherent relationship was established between the two assemblages. The second section of the thesis aimed to do this by comparison of the contemporary and sub-fossil data. All fossil and sub-fossil assemblages are fragmentary as there is differential preservation between species. It has been reported that key species, particularly *Daphnia* are not represented in sedimentary assemblages (Frey 1960, Korhola & Rautio 2001). Ephippia can, however, be identified to species level in the case of *D. magna* and to species aggregates for other groups such as *D. hyalina* agg. As a result ephippia have been used in a number of relatively recent studies (Jeppesen et al. 1996, 2003a). Here, the sedimentary assemblages of chitinous and ephippial remains were combined in order to provide some representation of *Daphnia* and *Ceriodaphnia*. A comparison of the data sets revealed differences in the relative abundance of species in the contemporary and sub-fossil assemblages resulting, in part, from the fact that sedimentary counts represent a spatial and temporal integration of contemporary communities.

Given, the inevitable difference between the two sets of zooplankton data, a more appropriate comparison of the relationship between the assemblages and their structuring forces was conducted. This employed CCA, redundancy analysis (RDA), Procrustes rotation and the related PROTEST (Peres-Neto & Jackson 2001). These analyses demonstrated that the two assemblages were structured by the same forces, chiefly ZF and APVI and to a very similar degree. Thus, it could be concluded that both the living and the dead communities reflect the environment they are shaped by in broadly the same way.

Establishing that the sub-fossil assemblages are shaped by the same forces to a similar magnitude as the contemporary community provides greater confidence in the interpretation of changes in fossil assemblages. In addition it demonstrates the validity of the using surficial sediment assemblages to construct models with which to track changes in the contemporary environment.

Section 3 - The first two sections of the thesis established that a combination of factors determine whole community composition and the likelihood of occurrence of individual species. This precluded the use of the transfer function approach to palaeoecological inference modelling as it contravened one of its key assumptions, namely, that environmental variables, apart from the variable the value of which is being modelled, have no significant effect on the assemblage (Birks et al. 1990, Juggins 1992). Thus, established modelling techniques, such as weighted averaging (WA) (e.g. Birks 1995) and weighted averaging partial least squares (WAPLS) (ter Braak & Juggins 1993), for defining a species' optima and tolerance and inferring past changes in one chemical or biological parameter in isolation were likely to be inappropriate for the data set presented here. In their place a semi-quantitative approach was used employing multivariate regression tree (MRT) analysis to identify critical values or 'break points' in ZF and APVI associated with shifts in the sub-fossil cladoceran assemblages. This MRT identified six groups of sites with significantly different sub-fossil cladoceran assemblages each delimited by distinct ranges of ZF and APVI. The veracity of the model was assessed by comparing the observed versus predicted group membership. This was achieved using RDA of the cladoceran data constrained by ZF and APVI, but in addition the sites were placed passively within the analysis. Thus, there was both a fitted and non-fitted value for each site providing an error component to the model. Notwithstanding some error in the model group membership, which ascribes a range of ZF and APVI values, was relatively reliably predicted. The model, therefore, demonstrated that sub-fossil cladoceran assemblages appear to reliably reflect the ZF density and APVI of shallow lakes, but that prediction of precise values may be impossible due to inherent noise in biological data. In addition the MRT groups had distinct ranges of TP, nitrate, Chla and August SD. This suggested that the groups reflected different forms of ecological structure and function.

Section 4 – The final part of the study consisted of the analysis of cladoceran assemblages in the sediment cores from two shallow lakes. These lakes were Felbrigg Lake, which formed part of the model training set, and Kenfig Pool, which was not in the training set. Both lakes were known to have undergone significant changes in their biological structure over the last century.

The sedimentary cladoceran assemblages show that Kenfig Pool underwent a dramatic change at around 50 cm, (c. 1850) with a change from a benthic to a more pelagic community, which may have been precipitated by a change in lake level. There was a subsequent, more gradual change, post 1950. In order to reconstruct changes in MRT group membership and to provide an indication of relative change between samples the fossil cladoceran assemblages were passively placed in an RDA of the training set sites constrained by ZF and APVI (section 3). The movement within the biplot reflected temporal shifts in the ecological structure and function of the sites. Notwithstanding a large shift in the time track at 50 cm there was no change of MRT group at Kenfig Pool as the site retained clear water, dominated by submerged plants and with low ZF. There have been well documented manipulations in the fish community at Kenfig Pool which appear to be accurately reconstructed by the cladoceran record, as the site progressed from a low ZF, through intermediate, to high ZF density over the last 50 years.

At Felbrigg Lake there have also been marked changes in the cladoceran stratigraphy. The reconstruction of MRT group membership displayed some dramatic changes, in particular, towards the top of the sequence. There was an initial period of stability at the base of the core, where the MRT group indicated high APVI and relatively high ZF density. In the late 19th century there was a relatively large shift within MRT group B concurrent with the loss of *M. spicatum* and a decline in *Chara*. In the late 20th century the MRT model indicated large variation in the ZF abundance and a decline in APVI. Historical and anecdotal records of fish community composition point to a sustained period of instability in the fish community with the loss of the dominant zooplanktivore (small perch), the proliferation of other species and the eventual rise in numbers of an alternative zooplanktivorous species (rudd).

For both the sites plant macrofossil data were available and provided further information of shifts in the biological structure of the sites. In similar small shallow lakes the sedimentary remains of aquatic plants have been shown to accurately reflect shifts in the dominant components of the aquatic flora of a site (Davidson et al. 2005, Zhao et al. 2005). At the two lakes alterations in ecological structure and function reflected by changes in the cladoceran assemblage were mirrored by the changes in the plant macrofossil assemblage. This provided a further validation of the technique and suggests it provides a reliable way to semi-quantitatively reconstruct macrophyte abundance, and ZF predation pressure in shallow lakes. In addition, the MRT groups may represent distinct types of ecological function in shallow lakes. There may be potential for this technique to track shifts in the balance between benthic and planktonic primary production, associated with nutrient enrichment.

6.3 Sources of uncertainty

Sampling of any biological community introduces some form of bias. Indeed, there is no one technique for a sampling the zooplankton community which does not sample part of the population more effectively than an alternative technique (Bottrell et al. 1976). The use of two methods for sampling zooplankton was an attempt to obviate this problem. The quantitative estimation of fish populations, particularly in shallow, plant dominated lakes, is problematic, indeed it could be argued that all fish sampling techniques are semi-quantitative. The technique applied here, point-abundance sampling by electrofishing (PASE) (Perrow et al. 1996, Skov & Berg 1999) has been shown to be particularly effective in sampling the dominant small fish (<10 cm) of vegetated shallow lakes, whilst still sampling larger individuals (Perrow et al. 1996). The results also compared well to an alternative method employed at 15 of the sites, where stop nets and electrofishing were used to sample discrete areas of the lake (Jones & Sayer 2003). Given the focus of the study and the nature of the lakes PASE was probably the most appropriate technique available. Whilst, the precise quantification of fish density may contain a relatively large amount of uncertainty the results suggested that there was good consistency of results between the sites. The analysis of contemporary zooplankton species distribution, in particular,

suggested that the sampling technique had provided relatively good estimates of ZF density. Thus, whilst the absolute estimates inevitably contain some error, the values relative to each other appear to provide a good estimation of the predation pressure exerted by the fish community at each site. Nevertheless using complementary techniques, with gill-netting or fyke-nets in addition to PASE would have added a degree of confidence to the population estimates. The choice of numerical methods, in particular the MRT, also allows for a degree of uncertainly in the quantitative estimates of the environmental variables.

A further source of uncertainty is the degree of spatial heterogeneity of cladoceran surface sediment remains. One sample from a central lake position has been used repeatedly employed to characterise lake conditions and infer past change (e.g. Frey 1958, Boucherle & Züllig 1983, Jeppesen et al. 2003a). In this study a single sediment sample from the centre of the lake was employed and the results indicate that this is sufficient to characterise the ecological structure and function of the site. It is desirable, however, that the spatial patchiness of sedimentary remains in shallow lakes be investigated more fully in order to establish the degree of heterogeneity and perhaps to establish the most representative location.

6.4 Conclusions

The use of sub-fossil cladoceran assemblages to assess temporal variation in lentic ecosystems clearly has great potential. Notwithstanding some behavioural plasticity, the balance between the pelagic and benthic species appears to be particularly sensitive to alteration of trophic state. Furthermore, the change of the relative abundance of species within these functional groups provides information on top down pressures, in this study, vertebrate predation pressure. The semi-quantitative inference model developed here exploits these shifts in the sub-fossil cladoceran assemblage, whilst allowing for the inherent noise in biological and environmental data. The result is a robust model, which when applied to sedimentary data appears to be sensitive to alterations in ecosystem function associated with changes in macrophyte abundance and zooplanktivorous fish density.

6.5 Application to management

The method developed here, in particular when used in combination with other palaeolimnological indicators, such as plant macrofossils, diatoms and pigment analysis may provide information on the nature of ecosystem change resulting from eutrophication. This may help determine the causes and mechanisms which lead to the decline in water and ecological quality of aquatic systems resulting from nutrient enrichment. Furthermore, by analysis of sediment assemblages from pre-industrial periods it may be possible to determine the macrophyte and fish communities of shallow lakes in pristine conditions. Where these base-line or reference conditions are established then the degree of change can also be assessed. This is particularly relevant in the light of the requirements of the European Council (EC) Water Framework Directive (WFD) which requires some knowledge of past site condition and an assessment of any change from that state.

Other palaeoecological indicators, such as diatoms, have been employed to aid ecological status and reference condition assessments (Bennion et al. 2004). Reliance on only one indicator, especially in particular lake types (e.g. high alkalinity lakes, shallow lakes and marl lakes where diatoms may preserve poorly) has a number of weaknesses. There may be great potential, therefore, to combine a number of indicators, each affected by different aspects of environmental change, to provide a more holistic way to explore shifts in ecological structure and function.

The ecological state of shallow lakes ecological may remain unaltered by increasing nutrient concentrations as elevated TP concentration do not always lead to rise in Chla. Thus, whilst clear water and a diverse macrophyte assemblage may persist as nutrient levels increase the ecological functioning of a site may, however, change. The method developed here appears to be sensitive to such shifts in function. The changing zooplankton population may, therefore provide an early warning of a lakes increasing vulnerability to a regime shift.

6.6 Future directions

The approach to environmental reconstruction employed here represents a new way of inferring the past biology in shallow lakes. The validation of the model is a key step to proving its reliability. This could be achieved either through the testing against independently collected surface assemblages at sites with known fish and macrophyte density or through its application to assemblages from sediment core where past fish and plant communities are known. A site in the Norfolk Broads with relatively long term fish and plant data would be appropriate. The management practice of sediment removal has however, limited the number of options in that region. The application to core material in chapter 5 represents a partial validation. The plant macrofossil and fish stocking data did not, however, provide absolute values of past APVI or ZF density. Although every effort was made to include lakes with low nutrient concentration in this study, there was still a dearth of sites at the very low end of the trophic gradient. The relative paucity of such sites in lowland Britain and Denmark made it difficult to locate such sites. The study would, however, have benefited from the additional of a greater population of relatively un-impacted sites, perhaps, increasing the sensitivity of the model to the first stages of eutrophication. Thus, the model may be improved by the addition of more sites in the training set, in particular it may benefit from increasing the number of sites with low nutrient concentrations.

Another direction which may improve the reliability of inference models is the inclusion of data on the morphology of sedimentary remains. For example, the size of *Daphnia* ephippia and aspects of *Bosmina* remains, such as antennule length, have been shown to reflect fish predation pressure (Jeppesen et al. 2002, Kerfoot 1981). The integration of morphological and species composition data into a single model may allow more confident and sophisticated modelling of change in predation pressure, perhaps even including invertebrate predation.

Further investigation of benthic species is required to determine more clearly habitat preferences. The data presented here (Chapter 2) hinted at an element of size structuring by fish. Whilst Whiteside (1970) stated that benthic chydorids are unaffected by fish predation more recent work on a range of benthic invertebrates, including some chydorids has suggested that some size structuring occurs (Blumeshine et al. 2000). The effects of invertebrate predation are also likely to be influential and shallow lake studies would in general benefit from the integration of more invertebrate data.

The use of sub-fossil cladoceran assemblages may not be limited to detecting the impacts of eutrophication on shallow lakes. Any factor that alters food web structure or trophic state should effect cladoceran species composition. Thus, there may be potential to apply these analyses to detect the impact of climate change. For example, increased growing season length at higher latitudes and altitudes resulting from climate change is likely to have altered ecosystem structure and function. This may well affect the benthic and pelagic productivity and would thus be reflected by the cladoceran assemblage.

As palaeoecological techniques become more sophisticated, it is their use in combination with contemporary ecology and limnology that may prove the most interesting. There has been an increasing amount on research focussing on shallow lakes in the last few decades with a wealth of contemporary studies (e.g. Moss 1977, Scheffer et al. 1993, Jeppesen et al. 2000, Vadeboncoeur et al. 2003). The meaningful interpretation of palaeolimnological data relies to a very large degree on such contemporary studies. Crucially, however, the longer term perspective provided by analysis of sedimentary material may provide insights into processes occurring on inter-annual or decadal time scales. For example the development of an ecological theory or principal based on contemporary sampling of a year may not detect a longer term trend masking the actual process at work. Although eutrophication is a relatively old problem further work is needed on determining the actual mechanisms of plant loss in shallow lakes. This study has indicated, at Felbrigg Lake, that alteration in ecological function may precede any change in ecosystem state. It seems therefore that the application of palaeolimnology may throw up questions that only modern limnology or its combination with palaeolimnology can answer. For example a change in macrophyte community composition and abundance appeared to occur at the onset of eutrophication (Moss 1989). However, was it the alteration of the balance of benthic-pelagic primary

production that caused this or an increase in the load of epiphytic algae on macrophytes? Is this detectable by analysis of just chlorophyll-*a*? Or do the herbivore communities need to be included? It may be that the combination of robust palaelmnological techniques and contemporary ecological investigation of shallow lakes is the most apposite way of addressing such question.

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